THE CAPACITY OF VISUAL SHORT TERM MEMORY DETERMINES THE BANDWIDTH OF INFORMATION TRANSFER INTO VISUAL LONG TERM MEMORY

by

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A DISSERTATION

Presented to the Department of Psychology
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy

June 2012

DISSERTATION APPROVAL PAGE

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Title: The Capacity of Visual Short Term Memory Determines the Bandwidth of Information Transfer into Visual Long Term Memory

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Degree awarded June 2012

DISSERTATION ABSTRACT

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Doctor of Philosophy

Department of Psychology

June 2012

Title: The Capacity of Visual Short Term Memory Determines the Bandwidth of Information Transfer into Visual Long Term Memory

Visual long term memory (VLTM) research has shown that we are capable of learning a virtually infinite amount of visual information. At the same time, visual short term memory (VSTM) research has shown that there is a severe limitation in the amount of information we can simultaneously apprehend at a given time. How does the severe capacity limitation in the initial uptake of information influence the encoding of information into VLTM? To this date, there has been no direct test of such influence, and the effect of such limitation has been unclear. Here, we demonstrate that, across wide varieties of conditions, the severe-capacity limitation in VSTM dictates the encoding of information into VLTM by determining the "bandwidth" of information transfer. This finding has a substantial implication for the understanding of the role of severely-capacity limited VSTM in forming many types of VLTM representations.

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Fukuda, K. & Vogel, E. K. (2009) Human variation in overriding attentional capture, *Journal of Neuroscience, 29*(27), 8726-8733.

ACKNOWLEDGMENTS

I could not have completed this dissertation without the great support from many people. First of all, I could not have been any more fortunate to have Ed Vogel as my mentor. Ed has provided tremendous and continuous support for every aspect of my undergraduate and graduate carrier as a researcher, and I hope to continue to work together as we keep trying to deepen our understanding of human cognition. I would also like to thank my dissertation committee: Ed Awh, Nash Unsworth, and Cris Niell for providing me with critical yet supportive evaluations of my projects. Especially, I am very thankful for a series of conversations with Ed Awh that provided me with many helpful insights for conceptualizing the findings. Needless to mention, my graduate carrier couldn't have been this exciting and meaningful without any of Vogel and Awh lab mates. I thank Trafton Drew, Veronica Perez, Andrew McCollough, Nathan Ashby, Roy Luria, Hiroyuki Tsubomi, Edward Ester, David Anderson, Richard Matullo, Irida Mance, Brittany Dungan, Atsushi Kikumoto, Karl Friedrichsen, and Dan Klee for helping me in all phases of this dissertation and other projects from designing experiments, running experiments, sharing the aaahs and ooohs of data interpretation, cleaning the caps, to revising and formatting this dissertation (special thanks to Richard and Brittany). Finally, I would like to thank my parents and my family, Tomoko, Kye, and Kou for providing emotional support through joyful home that always comforted and motivated me during the six years of graduate school.

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CHAPTER I

THE DUAL MEMORY SYSTEM AND MODAL MODEL

INTRODUCTION

There is no doubt that we rely on past experiences in every aspect of life. What makes a past experience meaningful is our powerful ability to store the experienced information in memory so that it can be accessed later to guide our behaviors. Therefore, how memory is instantiated and how information is encoded into memory has been the central issue for the field of philosophy, psychology and more recently, neuroscience. In this first chapter, I will first go over the discrete nature of our memory systems, and then discuss how such structural characteristics have been examined to better understand the process of memory acquisition.

THE DUAL MEMORY SYSTEM

We have countless memories from our childhood (e.g., the faces of your friends and teachers in the middle school, the pet dogs you used to have), and if we are asked about them 5 years from now, we would probably be able to recollect them. This ability suggests that we are capable of storing virtually infinite amount of information over a number of years. At the same time, however, such memories might require effortful search for retrieval (e.g. where you parked your car this morning). This massive collection of information is termed “memory proper” or secondary memory (SM). On the

other hand, memory is also at work for much shorter spans of time. For example, imagine that you want to call a restaurant to order a dinner. You would have to look up the number on the phonebook and remember it until you dial it. You would have little difficulty remembering the number, and keep the memory readily accessible in mind until you make the call. However, if your friend asks for the number an hour later, chances are that the memory is no longer present in your mind and you would need to look it up again. Also, if the phone number were 20 digit long, you would have a very difficult time remembering them and you might have to rely on some external memory device such as a paper and a pencil. These functional contrasts with SM (i.e. massive and durable but search-requiring memory) led William James (1890) to propose a separate type of memory (primary memory) that is limited in capacity and transient, but readily accessible.

Primary memory

The concept of primary memory (PM) has been confirmed and further refined by a number of experimental psychologists. One distinctive feature of PM is that it has a severe limit in the amount of information that can be simultaneously maintained. One traditional way to test this capacity limit is by presenting a string or an array of materials to remember, and record how many of them individuals can maintain after a short retention interval. A number of studies have examined its capacity across different types of inputs, and have reported a consistent result that normal individuals can hold 3 to 4 chunks of information (see Cowan 2001 for review). Here, a chunk can be a single item (e.g. a word) or an assembly of them so long as the items can be "chunked" in some

coherent manner. For example, three letters can be treated as three separate chunks, but when the three letters happen to form a semantically consistent unit (e.g. F, B, and I as in the "FBI"), the three letters can be treated as a single chunk. Some researchers even reported that the size of the semantic chunk could grow as large as a sentence (Craik and Masani 1967). Such semantic chunking can be extended to complex visual information. For example, chess experts can remember the spatial positions of multiple chessboards when the positions of pieces follow the chess rules (Chase and Simon 1973). Chunking can also be observed in perceptual levels. For example, three packman shapes can be treated as three separate items, but when they align to make an illusory triangle, it can be treated as a single chunk.

Another critical feature of primary memory relates to how information is lost. Information represented in primary memory has to be actively represented, or it is easily lost when the maintenance is disrupted. For example, when individuals are presented with a string of information to remember, they can recall back 3 to 4 chunks of information after a short delay. However, when subjects were engaged in some other cognitive tasks during the delay, their recall performance becomes worse monotonically as the function of the time spent on the secondary task (e.g. Peterson and Peterson 1959; Murdock 1961). This is strikingly different from the information stored in SM that can be retrieved regardless of the amount of time or the cognitive activities that have occurred after encoding.

Doubts about the dissociation

Although there seem to be several functional distinctions between primary

memory (PM) and secondary memory (SM), some researchers argued that memory system is better characterized as a single mechanism. They attempted to demonstrate the continuum by explaining the functional distinctiveness of PM by known SM properties. Melton (1963) wrote a review trying to examine if the rapid loss of information in PM due to maintenance disruption can be explained by interference, a well-known function of SM. Indeed, he found several situations in which interference built up as the function of (I) the number of items to be held in primary memory, and (II) the number of trials, and thus, the performance on PM task deteriorated (Murdock 1961; Keppel and Underwood 1962).

Crowder (1982) advanced these doubts by introducing studies that attempted to explain one of the traditionally-thought hallmarks of PM (i.e. the recency effect) with SM properties. In a typical immediate recall task, participants show a better recall performance for the last three to four items in a list compared to the items that preceded them. This is called the recency effect, and it has been shown to be robust against the manipulations influential to the secondary memory (e.g. presentation rate, meaningfulness of stimuli, etc). On the other hand, when participants' PM was occupied immediately after the encoding of items, the recency effect dramatically diminished (Glanzer and Cunitz 1966; Raymond 1969). Taken together, it has been thought that the recency effect emerges from preserved representations of last three to four items in PM. This inevitably suggests that the recency effect should not be observed when the items are no longer represented in PM. However, Crowder pointed out a situation where the recency effect was observed even though PM could not have held the items. Bjork and Whitten (1974) presented participants with a list of word pairs, one at a time separated by

12 seconds of arithmetic tasks. Participants were encouraged to rehearse only the word pair currently presented. After the list presentation, followed by 30 seconds of arithmetic, participants recalled the word pairs. If the recency effect is a reflection of sustained representations in PM, this procedure should wipe out the advantage for recently presented word pairs. However, they found a clear boost in the recall performance in the last word pairs, resembling the typical recency effect (Long term recency effect). This demonstration is particularly troublesome for theorists who based the distinctiveness of PM on the recency effect (Atkinson and Shiffrin 1971; Broadbent 1958).

Evidence for dissociation

As discussed above, behavioral evidence alone is not strong enough to support the validity of the distinction between PM and SM. However, it does not necessarily mean that PM does not exist. It only means that the functional distinction solely based on behavioral tendencies was premature. In fact, anatomical and neural evidence that supports the distinction are discussed below.

A subject H.M.: MTL as the key module for SM formation

When arguing that two cognitive systems are separable, no evidence is more powerful than showing distinct neural mechanisms for them. The best example that provides such a structural distinction between PM and SM is the well known amnesic patient, H.M.(Milner et al.1968; Milner 1972). H.M. suffered from severe amnesia after bilateral removal of tissues in the hippocampus. Even though he was able to clearly recollect memories encoded prior to the surgery, he was no longer able to explicitly recall

events that happened after the surgery. He was not able to recognize neighbors he had met repeatedly after his surgery, nor was he able to recollect the correct date and the time of the day. Explicit memory tasks also revealed no sign of training effects after hundreds of repetitions of trials. (Note that it was primarily the explicit memory tasks that revealed severe deficits. On the other hand, implicit memory tests showed some evidence of learning.) In sharp contrast to clear deficit in the formation of new memories (i.e. secondary memory acquisition), he showed normal PM capacity as measured by immediate memory tasks. Other studies of other amnesic patients showed very similar patterns of results. Baddeley and Warrington (1970) put six amnesic patients through a battery of PM and SM tasks, and found that amnesic patients had significantly worse SM compared to healthy controls in spite of relatively spared PM.

Based on the observations of H.M., researchers hypothesized that the medial temporal lobe including hippocampus was the central brain mechanism for the formation of SM. Indeed, many studies confirmed this hypothesis. For example, a number of monkey lesion studies found that just like H.M., lesioning MTL had detrimental effects on post surgery SM formation (Squire and Zola-Morgan 1983; Zola-Morgan and Squire 1985,1986). Also, a meta-analysis of two non-invasive human studies (Simons et al. 2001, Simons et al. 2002) revealed that the degree of atrophy on perirhinal cortex had a significant correlation with the performance on recognition memory tasks (Simons and Spiers 2003). Studies on healthy individuals also highlighted the importance of MTL region on SM functioning. More specifically, novel information that was successfully recalled later was associated with a stronger activation in the MTL regions during the encoding stage (Brewer et al. 1998; Wagner et al. 1998; Fernandez et al. 1999; Otten et

al. 2001; Davachi and Wagner 2002; Fernandez et al. 2002; Strange et al. 2002; Davachi et al. 2003).

Evidence of online maintenance of information in PM

Despite the severe damage on SM studies have reported that individuals with hippocampal damage have spared primary memory ability, consistent with H.M.'s observation. In fact, according to the review of 147 case studies of individuals with hippocampal damage, there has been no report of impaired primary memory capacity (Spiers, Maguire, and Burgess 2001). Another critical evidence about the existence of PM comes from neural studies. The most important criterion for PM is that it is an online memory system where memory contents are "actively" represented. This criterion is often overlooked in behavioral measures partly because it is very difficult to disentangle the influence of the offline storage of memory (i.e. secondary memory). In this sense, neural measures have a critical advantage because it can provide a direct observation of "active maintenance" while information is represented online without necessitating any behavioral outputs.

Initial evidence of the online maintenance of mnemonic representations was observed in monkeys. Goldman-Rakic and colleagues had monkeys perform a PM task called the delayed-match-to-sample task while recording the firing rates of neurons in the frontal lobe. In this task, monkeys were first presented with visual stimuli to remember over a blank retention interval, and when a test probe was presented, they had to indicate if the test probe matched with the initially presented stimuli. When the neural activities of frontal cells were examined, it turned out that cells that showed stimulus-specific activity

continued to fire throughout the retention interval (e.g. Funahashi, Bruce and Goldman-Rakic 1989).

In humans, similar observations were reported using the ERP technique. Vogel and Machizawa (2004) briefly presented colored squares bilaterally on the computer screen and asked participants to remember the squares on one side of the screen (Memory array). After a one second retention interval in which the squares were taken away from the screen, participants were presented with a test array that was either identical to the preceding memory array or that was different by one of the squares. Participants' task was to indicate if the memory array and the test array were identical or not. Behavioral performance on this task suggests that individuals can remember about 3~4 colored squares, nicely matching with the traditionally suggested PM capacity.

More importantly, they recorded online EEG while participants were performing this bilateral change detection task, and they found an electrophysiological signature of the "active" maintenance of information. More specifically, they found a sustained negative activity on the contralateral side to the memorized visual field (contralateral delay activity, or CDA) during the retention interval. Furthermore, the amplitude of CDA showed a linear increase up to individuals' PM capacity (i.e. set size effect), and it hit an asymptote for supra-capacity set sizes. Shortly following, the set size effect was also observed in an imaging study by Todd and Marois (2004). They had participants perform a change detection task while recording their hemodynamic response in the brain, and found that the BOLD response in posterior parietal cortex during retention interval showed a linear increase up until the set size was equal to 4, and it stayed constant when the set size exceeded PM capacity.

Summary

In summary, even though the initial functional distinction based on behavioral trademarks (e.g. recency effect in the immediate recall task for PM) turned out indecisive, neural studies clearly supported the distinct neural characteristics for PM and SM. More specifically, SM system has been shown to have a heavy reliance on the MTL structure, especially the hippocampus. Further, the fact that individuals who suffered from hippocampal amnesia have spared PM capacity added a credibility to the differential reliance of PM and SM on hippocampus. Neural studies also made a huge contribution to establishing the existence of PM. Specifically, the online maintenance of severely limited amount of information, the most important characteristics of PM, has been validated by both electrophysiological and neurophysiological activities. Taken together, the separability between PM and SM seems to be well-accepted in the field.

MODELS OF SECONDARY MEMORY ENCODING

The Modal model

Now let us turn to the key question of how memories are encoded so that it can be accessed later. At the same time as the validation of PM by experimental psychology, very influential models of memory encoding were introduced by Broadbent (1958), Waugh and Norman (1965), and Atkinson and Shiffrin (1971). These three models differed in details, but they all proposed three important assumptions. First, to encode information into a durable and long-lasting SM storage, it has to first go through PM.

Second, information in PM has to be continuously rehearsed or it will be lost. Third, the rehearsal mechanism in PM is the mechanism to transfer information to SM.

To validate this model, Atkinson and Shiffrin (1971) analyzed the behavioral performance of several well-known memory paradigms. In an immediate recall task, a list of words was sequentially presented, and immediately after the presentation, the words presented were recalled by participants. In this task, the typical finding is that participants are particularly good at recalling the words presented either at the beginning or the end of the list. In other words, the recall performance shows a characteristic U-shape function as the function of the serial positions of the words. The better performance in the early serial positions was termed as the primacy effect, and the better performance towards the end of the list was termed as the recency effect.

Atkinson and Shiffrin reviewed several studies that significantly contributed to the understanding of the primacy and the recency effect. First, the recency effect can be selectively eliminated leaving the primacy effect intact by introducing filler tasks (e.g. arithmetic problems) between the word presentation and the recall phase. This led the authors to argue that the better performance for the last words in the lists are because those words are still available in PM when recall is prompted. Thus, they interpreted the recency effect as the manifestation of PM.

Second, even though the U-shape function was still observable, the list length and the presentation rate impacted the immediate recall performance of all items prior to last several words in the recency range. More specifically, both elongating the list and speeding up the presentation lowered the recall performance of all the words except for the words in the recency range. Thus, they argued that the list length and the presentation

speed affected the recall performance when the word had to be retrieved from SM while sparing the recall performance for words remaining in PM.

Based on the assumption that the recency effect is a PM manifestation, and the primacy effect is a SM phenomenon, they claimed that rehearsal in PM is an important mechanism to encode information into SM. More precisely, they argued that the serial position function of the immediate recall performance could be explained by the amount of rehearsal executed for each word. For example, when the first word "cat" is presented, participants would rehearse "cat" repeatedly until the second word "dog" is presented. As soon as "dog" is presented, participants would start rehearsing "cat" and "dog" until the third word "chicken" is presented. When "chicken' is presented, not surprisingly, "chicken" enters the rehearsal loop. This simple addition of new words to the rehearsal loop continues until PM capacity is full, and at that point when the next word is presented, one of the words in the rehearsal loop is replaced by the new word. Thus, when the presentation is complete, the initial words in the list ends up with substantially more rehearsal counts than other words in the list that have relatively equal rehearsal counts. This function of rehearsal counts nicely replicated the recall function except for the last several items in the list for which recall performance was boosted by the available representation in PM.

Despite the elegance of the theory, it is impossible to count the number of covert rehearsal during the immediate recall task. Here, they cited a study with an immediate recall task in which participants were asked to overtly rehearse the presented words (Rundus 1971). In this study, participants were asked to covertly rehearse the words that were available to them during the sequential presentation of the word list. This study

revealed three important observations. First, the number of items contained in the rehearsal loop increased until the fourth word was presented, and after that, the number of words in the loop remained constant irrespective of the number of words presented. Second, participants almost exclusively reported the words in the most recent rehearsal loop when prompted to recall the words. Third, when the rehearsal counts were analyzed as the function of the serial positions, the first several words, indeed, had substantially more counts than other words in the list that had relatively constant rehearsal counts. Not surprisingly, the function of rehearsal counts perfectly traced the serial position curve of the recall accuracy except for the recency portion of the curve.

In the following experiments, the rehearsal count was directly manipulated to further test the role of rehearsal in encoding of SM. In a one-item condition, participants were trained to covertly rehearse the most recently presented word three times until the next word was presented. This assured that each word was rehearsed only three times regardless of its serial position. After the presentation, they probed the recall performance twice; immediately after the list presentation, and at the end of the experiment. For the immediate recall task, they successfully eliminated the primacy effect. More specifically, the immediate recall performance was constant except for the last several items that showed the recency effect. In final recall, they again showed no long term primacy effect.

In another condition, they manipulated the repetition counts for different portions of the serial positions. When the first word was presented, subjects were instructed to rehearse the first word three times. When the second word was presented, they were instructed to rehearse the second word twice and the first word once. After the third word was presented, they were instructed to rehearse most recent three words one time each

until the next word was presented. This manipulation allowed the first word to be rehearsed 5 times in total, the second word to be rehearsed 4 times, and all the rest of the words to be rehearsed 3 times except for the last two words: the second to the last word was rehearsed once, and the final word only once. In this condition, both immediate and final recall showed the primacy effect driven by the first two words that were rehearsed more than the others. Further, the final recall showed negative recency effect. More precisely, the last two words that were less rehearsed were less likely to be recalled. Based on the results of Rundus (1971), Atkinson and Shiffrin proposed two functions of rehearsal. First, rehearsal was the mechanism to maintain information in PM, and second, rehearsal was the mechanism to transfer information to SM.

Criticism to the Modal model

Conflicting evidence for the role of rehearsal

Although the modal model seemed very reasonable given its explanatory power for traditional memory tasks, the model has been questioned by several critics using various paradigms. The first major criticism pertained to the pivotal function of rehearsal. As introduced earlier, rehearsal plays the fundamental role in the modal model for it is thought to enable information to linger in PM, and to enable the information to be transferred to SM. However, Craik and Watkins (1973) presented directly opposing evidence demonstrating that the number of mere rehearsals did not play a role in transferring information into SM. In their study, participants were first assigned with a critical letter (e.g. “g”), and their task was to remember the most recent word that started

with the critical letter in the list of words that they were then presented with. For example, first, a participant was given the critical letter "G". Then, a list of words were spoken to the participants as follows; "Guitar", "Cat", "Dog", "Gun", "Goose", "Ball", "Tape", "Pen", "Apple", "Game".... When "Guitar" was spoken, participants were supposed to maintain the word "Guitar" since it starts with the critical letter "G". When "Cat" and "Dog" were presented, participants had to keep holding "Guitar" in their PM presumably by covertly rehearsing "Guitar". As soon as they heard "Gun", they were supposed to drop "Guitar" from PM, and instead load "Gun" into their PM. However, since the next word "Goose" again started with the critical letter, they immediately had to switch the PM content to "Goose". "Goose" was maintained in their PM until the next critical word "Game" was presented.

This experiment allowed the direct manipulation of the duration of maintenance in PM, and thus, the duration of covert rehearsal for each item. For example, "Goose" was twice as long maintained/rehearsed than "Guitar" since there were twice as many intervening words presented until the next critical word was presented. According to the modal model, "Goose" should have higher chance of being stored in SM than "Guitar". To verify this, the authors administered a surprise recall test at the end of the experiment, and analyzed the recall performance as the function of the duration of maintenance rehearsal in PM. Surprisingly, the result showed no hint of PM maintenance rehearsal affecting SM transfer. More precisely, the number of non-critical words following the critical word had no effect on the performance of the final surprise recall test.

In the second experiment, they further tested the effect of overt rehearsal by examining the negative recency effect in a final recall task. As introduced earlier, the

negative recency effect is defined as the worse performance in a final recall task for the items that showed the recency effect in an immediate recall task administered previously. The modal model explanation for this is simple. The words presented towards the end of the list were less rehearsed, and therefore transferred to SM to a lesser extent. If that was the case, the negative recency effect should be reversed by selectively increasing the number of rehearsal for those words. Craik and Watkins tested this directly by asking participants to overtly rehearse the last four words as many times as they did for the first four words in the immediate free recall task. After 2 minutes of irrelevant conversation, subjects were then given a surprise final recall task. Here if the modal model was correct, the last four items should have been recalled with the same accuracy as the first four items. However, there was no hint of such an effect. It was only the first four words that showed better recall performance than other words that were equally poorly recalled. These results clearly suggest that the simple duration of PM maintenance, or the sheer number of rehearsals, has a negligible effect on SM encoding.

Patient K.F.: Intact SM with impaired PM

More evidence against the modal model came from the case study of K.F. who seemed to have damaged PM with spared SM. This immediately raises a problem to the modal model. That is, If information has to go thorough PM to be transferred to SM, how can individuals have spared SM with dysfunctional PM? The patient K.F. suffered from strokes that damaged the surface of left parietal lobe (i.e. perisylvian damage). Several investigations on this patient discovered that K.F.'s short term memory was severely impaired. Warrington and Shallice (1972) put the patient through several traditional PM

tasks, and here to illustrate his deficit in PM, two tasks are reviewed below.

In a free recall task, it is well known that normal individuals show a robust recency effect across the last four to six items in the list, and as we introduced, the range of the recency effect is often taken as the index of PM capacity. When K.F. performed this task, his recall performance indicated that he was only able to recall the last item on the list.This suggests that his PM capacity was as small as 1 item.

To further characterize his PM deficits, the researchers administered the Peterson procedure. In the Peterson procedure, participants are first given verbal items to hold in PM followed by a filler task that prevents participants from rehearsing the items for a certain time period. By examining the decline in performance, the decay function of PM is characterized. Previous observations revealed that the amnesic patients with impaired SM show a normal Peterson decay curve (Baddeley and Warrington 1970), which in turn suggests spared PM for amnesic patients. When K.F. performed this task, the performance was greatly reduced, and the decay was much quicker than typically observed. This again demonstrates the severe impairment of K.F.'s PM.

Given such severe deficit in PM, the researchers hypothesized that K.F. might be utilizing SM to compensate for poor PM in situation when normal individuals would only utilize PM. If that was the case, K.F.'s performance on a typical PM task should show characteristics specific to SM such as proactive interference. Proactive interference is defined as the deterioration of recall performance due to built-up interferences from proceeding trials.

To test this hypothesis, a digit span task was administered. In this task, ten series of ten pairs of letters were vocally presented. Two letters in each pair was presented

sequentially separated by 1 second, and then recalled within 5 second. The next pair followed immediately until the end of the series. Each series was separated by a one minute rest period. When K.F.'s recall performance was analyzed as the function of serial positions in the series, his performance declined towards the end of the series, thus showing the proactive interference. This confirmed the researcher's hypothesis that K.F. utilized SM to compensate for his dysfunctional PM.

On the other hand, despite his severely damaged PM, K.F.'s SM was demonstrated to be relatively intact. For example, when he was sequentially presented with a list of 10 words to learn, it took him 7 repetitions of the presentation before he was able to report back all 10 words. Control participants on the other hand, took 9 repetitions to achieve the same level of learning. These findings were interpreted as a severe criticism to the modal model since it suggests that SM can be formed even with severely-impaired PM.

Current view on the Modal model

In the previous section, two major threats to the modal model were reviewed. Do they mean that PM plays no role in SM formation? We would argue that it is too shortsighted to abandon the very intuitive framework that the modal model introduced. For example, K.F.'s observation that he had severely damaged PM with intact SM might seem crucial to the involvement of PM in SM formation. However, a closer look at K.F.'s case revealed that such a statement was an oversimplification in two ways. First, even though K.F.'s performance on auditory span was severely impaired, his visual span performance was relatively intact. Additionally, later studies showed that perisylvian

damage causes not only verbal PM deficits but also phonological processing deficits in general (Martin 1993). This leads to the possibility that the locus of the PM deficit observed in K.F. was not at the reduced PM capacity per se, but at the impaired phonological processing that hindered the phonological encoding of information. Second, when K.F.'s SM was examined, the stimuli used (e.g. visually presented words) allowed multiple encoding strategies (e.g. visual encoding, and semantic encoding) that were not allowed in verbal PM tasks. Given the profound deficit in phonological processing, it seems plausible that K.F. relied on other strategies that were functional. In fact, later studies of patients with perisylvian damage revealed that they did show SM impairment when stimuli can only be encoded in auditorial fashion (Ranganath and Blumenfield 2005).

The other severe critique about the modal model referred to the assumptions about rehearsal. The modal model assumes that the rehearsal is a unitary mechanism that enables both maintenance of a representation in PM and transfer of information to SM. Craik and colleagues effectively criticized such assumptions. First, they showed that there exist two functionally separable rehearsals (i.e. Type-I and Type-II rehearsal). Type-I rehearsal was defined as a rather automatic rehearsal of information during which information is evaluated rather shallowly (e.g. phonologically). Type-II rehearsal refers to a more elaborative rehearsal thorough which information is more deeply processed (e.g. semantically). Based on this distinction, they argued that only the Type-II rehearsal contributes to the transfer of information to SM. However, it is very important to note that the levels-of-processing view does not negate the information transfer from PM to SM. In fact, they even acknowledged the possibility that information that can be

processed in Type-II fashion is severely limited. Thus, even though the assumption that rehearsal is a unitary process that is critical to SM formation was too simplistic, the role of PM as the gate to transfer information to SM has not been denied. In the next section, more recent works investigating the role of PM in SM formation are reviewed.

Reassessment of PM maintenance

There is no doubt that how deeply information is processed has a profound impact on the successful transfer of information into durable SM storage (i.e. the levels of processing effect). Information that was processed to deeper levels is more likely to be transferred into SM than information that was shallowly processed. However, such a comparison largely by definition is blind to the contribution of simple maintenance of information in PM. To critically evaluate the effect of such contribution, one has to test if information that was simply maintained in PM left "any" memory trace or not. In fact, even in Craik and Watkins (1971), information that was simply maintained in PM was reliably recalled.

The other potential factor that could prevent the effect of simple PM maintenance from being observed is the type of test used to examine the SM trace. Traditionally, recall tests have been the standard test used to evaluate if information was transferred to SM. However, recall tests are known to be high-threshold tests of memory since successful recall requires the re-generation of the memory, and thus, researchers agree that recall is rather insensitive to the existence of memory traces. On the other hand, a recognition test relaxes its requirement for successful performance by providing a cue for which subjects simply have to indicate if the cue is present in memory or not. In such sense, recognition

tests are more sensitive measures of the existence of any memory trace. In fact, some researches that have used recognition tests as the index of SM formation did find the contributions of PM maintenance that were arguably executed in the Type-I fashion (Woodward et al. 1973; Glenberg et al. 1977).

Naveh-Benjamin and Jonides (1984a) examined the role of maintenance rehearsal in SM formation. Maintenance rehearsal refers to the simple maintenance of information in PM across the delay without further elaboration of the information. In the levels-of-processing model, it is consistent with Type-I processing. In their experiment, participants first performed a variant of Brown-Peterson task. In this task, they were first presented with 2,3, or 4 two-digit numbers to remember. After the presentation of digits, a pair of words was presented, and participants were asked to overtly rehearse them for 1,5 or 10 times. After the rehearsal was complete, participants were tested on their memory of the digits. Upon completion of 86 trials, participants were given a surprise recognition test for the words that they had to rehearse. In each trial of the recognition task, participants had to discriminate the target word from four lure words that included a synonym and a rhyme of the target. This task allowed the researchers to examine the effect of maintenance rehearsal when participants devoted arguably minimal mnemonic effort to the rehearsed words (thus minimal elaborative Type-II processing) in the face of the demanding maintenance of the digits. Furthermore, the analysis of errors in the recognition test enabled the researchers to characterize the nature of the memory traces left by the maintenance rehearsal.

The analysis of the surprise recognition test confirmed the involvement of the maintenance rehearsal in SM formation. First of all, across all load conditions,

participants were able to identify the words rehearsed reliably above chance. A further analysis for each load condition revealed specific details of its involvement. When participants concurrently retained 2 two-digit numbers (load 2) in memory, the recognition accuracy for the words linearly increased as the number of rehearsal counts increased. In the higher load (load 3 and 4) conditions, even though the specific correlation between recognition accuracy and the rehearsal count was not observed, the rehearsal count did impact the types of errors that participants made. More precisely, participants made more errors by choosing the rhyming lures as the rehearsal count increased. This suggests that the act of rehearsal even with arguably minimal mnemonic effort did leave a durable memory trace at the very least, at the articulatory level. Taken together, they interpreted that the sheer act of representing information in PM through rehearsal does contribute to the formation of SM, and that elaborative processing acting upon those PM representations strengthens the memory trace so that they can be better accessed.

In the following study (Naveh-Benjamin and Jonides 1984b), they further characterized the maintenance rehearsal by introducing the two-stage model of rehearsal. The two-stage model of rehearsal proposes that maintenance rehearsal can be broken down to two stages: an initial attention-demanding phase in which maintenance rehearsal is programmed up so that information can be sustained across a delay interval, and a following rather automatic phase in which programmed rehearsal is executed until the delay interval ends. They further claimed that it was the initial phase that primarily contributes to SM formation. To test this model, the researchers further elaborated on the paradigm introduced earlier in the following manner. Participants were first presented

with three 2-digit numbers to maintain. Immediately following, a pair of words were presented and participants were asked to rehearse them 1,4 or 10 times, after which the memory for the 2-digit numbers were tested. In addition, to measure the allocation of attention throughout the maintenance rehearsal, in two thirds of trials, a visual probe was presented either at the early, the middle, or the late portion of the rehearsal phase, which participants had to detect as quickly as they could. If attention was indeed diverted to maintenance rehearsal, a slowing in reaction time should be observed for the probe detection. After completing 130 trials, participants were given a surprise cued recognition test of the word pairs that they had to rehearse. The performance on this task was contrasted to the performance of a different group of participants who were informed in advance about the final recognition test and therefore rehearsed the words in a more elaborative fashion (i.e. Type-II processing).

The contrast supported the two-stage model of maintenance rehearsal. First, the analysis of probe detection RT showed that, in the incidental learning condition, when probes were presented at the early or middle portion of rehearsal, RTs were indeed longer when compared to the probe presented during the later portion of rehearsal. This suggests that the earlier stage of maintenance rehearsal did require attentional resources compared to the later stage of the rehearsal. On the other hand, the intentional learning condition revealed no such effect. The analysis of cued recognition performance added further support in the following manner. In the incidental learning condition, the cued-recognition performance improved as the rehearsal counts increased up to four times. However, further increases in rehearsal count failed to improve the performance. This finding was in sharp contrast with the trend observed in the intentional learning condition

that cued-recognition performance monotonically increased as the number of rehearsal counts increased. Thus, the researchers concluded the sheer act of maintenance does have an impact on SM formation with a strong emphasis on the initial attention-demanding stage in which maintenance is programmed.

Neural evidence in support of the Modal model

Recent neural studies added further credibility to the involvement of PM maintenance in SM formation. Using EEG, ERP and fMRI techniques, studies have found that neural activity during PM maintenance predicts later recognition performance of information that was stored in PM (Schon et al. 2004; Ranganath et al. 2005; Khader et al. 2007; Davachi et al. 2001; Axmacher et al 2008). Further, neural evidence that is in line with the two-stage model comes from recent fMRI studies. In 2006, Ranganath and colleagues have examined the neural activity during early versus late PM maintenance and their relationship with SM formation. In this experiment, participants were presented with a complex novel object to maintain in their PM for a short delay interval (7~13 seconds). After the delay, a probe item was presented, and the participants had to report if the probe was identical to the memorized object. The bold activities were recorded throughout the experiment. After the PM task, participants performed a surprise recognition test out of the scanner. To separate the neural basis of early and late PM maintenance, the BOLD responses were separately analyzed. Both the early and late maintenance period showed sustained activity across various brain areas including frontal and occipital areas. This suggests that a large network of brain areas contributed to the maintenance of information in PM (Ranganath and D'Esposito 2001). Interestingly, the

hippocampus also showed significant activation only in the early maintenance suggesting its involvement in the process of SM formation.

Next, to further support the two-stage model of PM maintenance, the BOLD activity during the maintenance period was binned based on the participants' performance on the subsequent surprise recognition test. When the BOLD activity was contrasted between the objects correctly recognized as seen and the objects that were not recognized, the activity in hippocampus showed a supporting evidence of the two-stage model. More specifically, the hippocampal BOLD activity in the early maintenance period was significantly larger for the objects that were successfully recognized in the subsequent test than those that were not. On the contrary, other areas that showed sustained activation throughout the delay period failed to demonstrate such sensitivity to the performance on the subsequent recognition. As a result, the close link between the hippocampal activity during the early maintenance stage and the recognition performance further supported the two-stage model of PM maintenance.

Another critical observation was obtained in a dual task situation. If PM maintenance is fundamental to SM formation, SM formation should be negatively impacted if PM is occupied by other information. Axmacher and colleagues (2009) tried to demonstrated a direct tradeoff between PM maintenance and SM formation by asking subjects to simultaneously perform both tasks in fMRI scanner. In this experiment, participants were asked to maintain a sequential presentation of four pictures across a short delay interval. The sequential presentations consisted of two load types: the low load sequence consisted of two novel shapes, one of which was presented three times and the high load sequence consisted of four novel shapes, each of which was presented once.

In other words, in low load condition, participants had to maintain the identities of two shapes, whereas in high load condition, they had to maintain four of them. In the middle of the delay interval, a picture of a face was presented and, subjects made an immediate gender judgment. After the delay period, participants' memory of the sequential presentation was tested. After the scan session was over, participants' memory for the faces introduced in the PM maintenance was tested by a surprise recognition test.

First of all, the results of the behavioral analysis revealed supporting evidence for such a tradeoff. Participants were significantly better at recognizing the facial pictures that were presented during the low load maintenance than those presented during the high load maintenance. This suggests that SM formation was hampered when PM was occupied with other information, and thus, less available. Neural data added further evidence for the tradeoff between PM maintenance and SM formation. First, when the BOLD activity during PM maintenance prior to the presentation of the facial picture was analyzed, the MTL areas (i.e. hippocampus, para hippocampal cortex) that are typically associated with SM formation showed a load effect. Specifically speaking, the high load condition showed larger BOLD activity across the delay interval than the low load condition. This, in line with other studies, suggests that the MTL region participates in PM maintenance. Next, when the BOLD activity during the facial judgment task was analyzed, these areas showed the inverse of the load effect. In other words, the MTL region showed more activity during and after the facial judgment task embedded in the low load condition than in the high load condition. This seemed to suggest that the PM maintenance load affected the degree to which MTL region can participate in SM formation of the facial pictures, and thus suggesting the common limited resource for PM

maintenance and SM formation.

Summary

In this section, we have reviewed more recent evidence that further sharpened the understanding of the role of PM maintenance in SM formation. Studies that utilized more sensitive behavioral measures of SM formation suggest the contribution of the sheer PM maintenance in SM formation. Further, the disproportionate contribution of the early rehearsal to SM formation led researchers to propose the two-stage model of PM maintenance. More recent neural evidence further buttressed the argument by showing that the neural activity during PM maintenance, especially the early maintenance, was predictive of successful SM formation. Taken together, it is evident that PM maintenance has a selective, yet direct role in forming SM.

GENERAL DISCUSSION

Memory helps us in every aspect of life. It enables us to learn new things so that we can better interact with outside world. Therefore, understanding the mechanism of memory has been the central topic for philosophy, psychology and neuroscience. In this chapter, we focused on the mechanism to encode information into durable storage (secondary memory) by introducing behavioral and neural evidence that helped to refine this rather intuitive modal model of memory. The modal model assumes that the information in the external world has to first enter the capacity-limited online memory system (primary memory or PM), and through maintaining information in PM, the

information is transferred into durable and massive memory storage (secondary memory, or SM).

This theory, despite its appealing simplicity, has been historically questioned by many theorists because of two major criticisms. First, the case study of patient K.F. who had a severe verbal PM deficit showed the normal functioning SM questioned the single pathway of information transfer from PM to SM. Second, the observation that sheer PM maintenance did not linearly improve individuals' ability to retrieve the maintained information in the surprise recall test caused severe problems for the modal model's interpretation of sheer PM maintenance as the unitary driving force for SM formation. However, recent studies revealed that these criticisms are not enough to abandon the framework that the modal model proposed for the following reasons. First, recent investigation suggests that the locus of K.F.'s deficit was for the vocal processes supporting the maintenance rehearsal rather than PM maintenance itself. Second, behavioral and neural evidence using more sensitive measures of memory traces revealed that PM maintenance, especially its initial portion, contributes significantly to the formation of SM. Further, a recent fMRI study suggests that there is a shared resource between PM maintenance and SM formation by demonstrating the direct tradeoff in behavioral performance as well as neural activities. Taken together, even though there is more work to be done to fully evaluate the PM's role as the gateway for SM formation, the more recent evidence so far strongly suggests that the framework proposed by the modal model is still useful to understand how information is transferred into the massive and durable storage of memory.

The goal of the dissertation

PM determines the "bandwidth" for SM formation

One important claim that the modal model proposed and left to be criticized by the levels-of-processing model is the capacity limitation of PM. It has been well demonstrated that there is a severe limit to the amount of information that can be held active in mind. The Levels of processing model does not explicitly discuss the functional importance of this severe bottleneck. In fact, it is entirely plausible that, consistent with the modal model, the severe bottleneck of PM capacity determines the amount of information that can be further processed either shallowly or deeply by participants' intention, and thus the levels-of-processing effect arises within the bottlenecked PM system. In this sense, the framework of the modal model can still be correct in that the PM serves as the gateway that information passes through so that further processing can be evoked to affect the SM formation. Though some suggestive evidence comes from recent fMRI studies, no studies so far have directly demonstrated such a link between the PM bottleneck and SM formation. Therefore, this will be the main focus of this dissertation (discussed in chapter 2).

The generalizability of the modal model to encoding of implicit memory

Another direction in which the modal model can be tested is the mechanism for the formation of implicit memory. The examination of the modal model so far has focused on memories that are explicitly retrieved (i.e. individuals had to explicitly judge if the presented information is remembered or not). At the same time, we know from the

literature that our past experiences can influence our behavior without reaching our awareness. For example, previously seen images can be identified faster than images that were never seen before (i.e. perceptual priming) even when individuals cannot explicitly recognize them. Alternatively, previously encountered items can bias the spontaneous generation of items for the related categories (i.e. conceptual priming). Past research has mainly focused on the dissociability of implicit memory from explicit memory, and indeed, many have found this double-dissociation between them in amnesic patients (Milner et al. 1968; Warrington and Weiskrantz 1974; Cohenand Squire 1980; Graf et al. 1984; Moscovitch1982; Schacter 1985) as well as in normal individuals (Graf et al. 1982; Jacoby andDallas 1981; Tulving et al. 1982; Blaxton, 1989; Roediger, Weldon, and Challis 1989; see Roediger 1990 for review). However, much less effort has been made to lay out the commonalities between them (Turk-Brown et al. 2006; Daselaar et al. 2006; Reder et al. 2009).

If PM serves as the sole gate for SM formation, implicit memory should also go through the bottleneck. At this point, no direct test of such a hypothesis has been reported, and evidence so far is ambiguous. Several studies in fact suggest the opposite (Bentin, Kutas, and Hillyard 1995; Isingrini, Vazou, and Leroy 1995; Jacoby, Woloshyn, and Kelley 1989; Kellogg, Newcombe, Kammer, and Schmitt 1996; Mulligan and Hartman 1996; Parkin, Reid, and Russo 1990; Parkin and Russo 1990; Russo and Parkin 1993; M. E. Smith and Oscar-Berman 1990; Szymanski and MacLeod 1996). For example, Isingrini and colleagues (1995) presented participants with words to remember while asking them to discriminate the letters that were concurrently presented. Even though this secondary task was attention demanding and negatively impacted

participants' ability to explicitly retrieve the words presented during the central task, it did not reduce the amount of implicit learning as measured by the category-examplar generation task for the target words.

On the other hand, some studies have indicated that, by exhausting the limited attentional resources, the amount of priming effect can be attenuated (Crabb and Dark 1999; Hawley and Johnston 1991; MacDonald and MacLeod 1998; Light and Prull 1995; Stone, Ladd, Vaidya, and Gabrieli 1998, Rajaram et al. 2001, Crabb and Dark 2003). For instance, Crabb and Dark (2003) has found that the amount of information that has to be simultaneously attended significantly impacted the amount of priming effect. More precisely, they presented 1,2 or 4 nouns briefly within which participants had to search for a named vehicle (e.g. truck). The analysis of the encoding task revealed that the detection accuracy decreased as the function of the load size. This is not surprising considering that the amount of limited attentional resource allocated for each word reduced as the total number of words increased. Following this encoding phase, participants were given the perceptual priming task in which they had to identify the words that were very briefly presented (i.e. 33 ms) and immediately masked. The amount of priming effect, calculated as the difference in identification accuracy between the old words (words presented during encoding phase) and the new words, showed a reliable reduction as the load size increased. This suggests that the priming effect is modulated by the amount of attentional resource available at the encoding phase.

As briefly reviewed here, a lot has to be done to conclude if implicit memory is formed through the capacity limited bottleneck proposed by the modal model. Thus, as the second goal of this dissertation, we sought to directly test the possibility of PM as a

common encoding mechanism for explicit and implicit memory (discussed in chapter 3).

CHAPTER II

VSTM CAPACITY DETERMINES THE "BANDWIDTH" OF VLTM ENCODING

INTRODUCTION

In this chapter, we focus on testing the primary, yet not directly tested, assumption of the modal model. That is, the amount of information that can be represented in primary memory (PM) at a time determines the amount of information that can be encoded into secondary memory (SM). To test this assumption directly, we need two types of information: the amount of information represented in PM during encoding and the amount of information successfully encoded into SM. In typical studies that tested the modal model, stimuli to be encoded were presented sequentially in isolation with enough temporal spacing to assure that each stimulus was studied sufficiently (e.g. Rundus 1971, Craik and Watkins 1973, Naveh-Benjamin and Jonides 1984a, 1984b and Ranganath et al. 2006). This procedure, however, makes it impossible to test the assumption of interest because the amount of information represented in PM is always constant during the encoding phase. Thus, rather than ensuring each stimulus is represented in PM to a certain criterion, we decided to modulate the amount of information represented in PM, and examine the consequent effect on the amount of information encoded in SM.

Visual Memory system as a suitable candidate system

For both tracking and modulating the amount of PM representations, we chose the visual memory system as the suitable model system. The PM for visual information, or the memory system that actively maintains visual information is conceptualized as visual short term memory (VSTM), and numerous studies have consistently shown its capacity, or the amount of information that can be simultaneously represented, is severely limited (Luck and Vogel 1997; Fukuda, Awh and Vogel 2010). Specifically, an average healthy young adult can only retain about 3 simple objects in VSTM at a given time. At the same time, we know that visual long term memory, or the secondary memory for visual information, can retain a virtually infinite amount of information (Brady et al. 2008). Taken together, both PM and SM for visual memory, VSTM and VLTM respectively, seem to provide a solid ground to investigate the assumption of our interest.

VSTM CAPACITY DICTATES VLTM ENCODING

General methods

In the first series of experiments, we sought to test the most basic corollary of the assumption. That is, if the amount of information represented in VSTM during encoding determines the amount of information encoded in VLTM, a larger amount of information in VSTM during encoding should lead to a larger amount of VLTM representations.

To test this corollary, it is essential to measure the amount of information represented in VSTM during VLTM encoding. We achieved this by implementing a standard VSTM task (i.e. the change detection task) in the encoding phase. In this task,

individuals were simultaneously presented with multiple objects to retain in their VSTM across a blank retention interval, after which,one of the objects was presented, and individuals were asked to judge if it was the same object presented at that location. Based on their accuracy on this task, we can estimate how many objects were retained in individuals' VSTM. Aside from the severe capacity limit of VSTM, we know that individuals widely, yet reliably, vary in the amount of information they can store in VSTM capacity; some individuals can retain as many as 4 objects, but others can retain as few as 2 objects at a time (Awh, Barton, and Vogel 2007; Fukuda et al. 2010). More specifically, all individuals have negligible difficulty in representing up to 3 objects in their VSTM. However, individuals start to show difficulty in representing all the items in their VSTM as the number of items (or the set size) exceeds their capacity. As a result, robust individual differences arise when the set size exceeds individuals' VSTM capacity (e.g. set sizes above 4). This pattern of results makes a straightforward prediction. If the set size is below individuals' capacity (e.g. set size 2), individuals should be equally good at encoding the stimuli into their VLTM regardless of their VSTM capacity. However, when the set size exceeds their VSTM capacity (e.g. set size 6), individuals should differ in the amount of information encoded into VLTM as the function of their VSTM capacity; high capacity individuals have more information encoded to their VLTM than low capacity individuals.

Experiment 1a and 1b: VSTM capacity dictates Object VLTM encoding

In Experiment 1a and 1b, we focused on the encoding of a relatively simple form of VLTM. That is the VLTM that enables individuals to judge if they have seen a picture

of an object or not (Object LTM). After measuring individuals' VSTM capacity using a standard color change detection task (see method), we put individuals in a VLTM encoding phase in which they performed an object change detection task. In this task, participants were simultaneously presented with either 2,4, or 6 pictures of objects to remember, and one of the objects was tested following the retention interval. After the encoding phase, participants performed a VLTM "old/new" recognition task. In this task, participants were presented with one picture of an object at a time at the center of the screen, and they were asked to judge if the picture of the object was presented anytime anywhere during the encoding phase. If VSTM capacity determines the amount of information encoded into VLTM, we would expect the following. For stimuli presented in set size 2 condition, high and low capacity individuals would be equally good at the VLTM task simply because both group can store 2 items in their VSTM. However, as set size increases, a positive relationship between VSTM capacity and VLTM performance would emerge because individual differences in VSTM capacity manifest themselves and become a determinant factor for VLTM performance. That is, those with high VSTM capacity will perform better on the VLTM task for items presented in higher set size condition (i.e. SS6). To anticipate the result, we ran the same experiment in both an incidental learning condition (i.e. individuals were unaware about the VLTM task, Experiment 1a) and an intentional learning condition (i.e. individuals were informed about the VLTM task prior to the VLTM encoding phase, Experiment 1b).

Participants

After signing the consent form approved by the IRB, 55 students (28 for

Experiment 1a, and 27 for Experiment 1b) with normal (or corrected to normal) vision at the University of Oregon participated for the introductory psychology course credits.

Procedure

1. VSTM task

A standard color change detection task was administered first to measure individuals' VSTM capacity (Figure 1). In this task, either 4 or 8 colored squares (1.15° x 1.15°) were presented for 150ms on the screen with a grey background (Memory array), and individuals were instructed to remember as many of them as possible over a 900ms retention interval during which the screen remained blank. Then, one colored square was presented at one of the original locations in the memory array (test array), and participants judged if it was the same colored-square as the original square presented at that location with a button press ("Z" if they thought it was the same, and "/" if different).

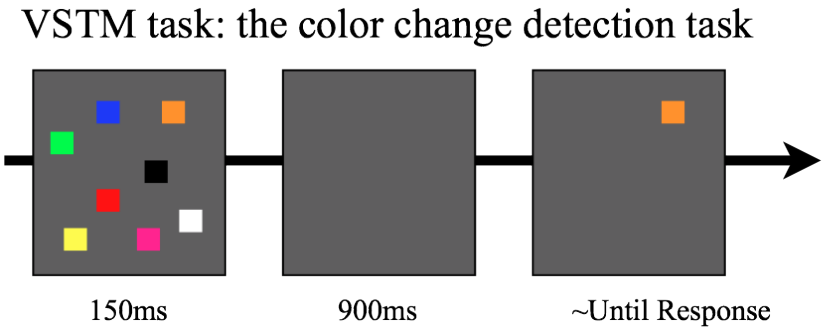

Figure 1. The change detection task
In this task, an array of colored squares is presented briefly, and participants are asked to hold it in mind during the retention interval. When a single square is presented, participants indicate if it is the same square as the one that was originally presented at that location.

The test array remained on the screen until their response. The change frequency was 50% to make sure that any response bias would neither benefit nor penalize their performance. The colors of the memory array were randomly selected from a highly discriminable set of 9 colors (red, green, blue, yellow, magenta, cyan, orange, black, and white) without replacement. Participants performed 60 trials each for set size 4 and 8 conditions in a pseudo-random order.

2. Encoding phase

After the VSTM task, participants performed an object change detection task (Figure 2). This task was identical to the color change detection task except for 2 changes. First, the stimuli presented were pictures of real objects (mean radius = 4.9°) borrowed from Brady et al. (2009), and second, the tested set sizes were 2, 4 and 6. Pictures were selected from a set of 2400 different pictures without replacement so that none of the pictures appeared on the memory arrays were presented more than once during the encoding phase. Participants performed 40 trials each for set size 2, 4, and 6 in a pseudo-random order.

3. VLTM test phase

Following the encoding phase, participants performed the VLTM recognition task (Figure 2.). In this task, participants were presented with one picture of real objects (mean radius = 4.9°), and they were asked to judge, with a button press, if it was a picture that was presented anytime anywhere during the encoding phase ("O" for "Old" or studied, and "N" for "New" or never seen) . The picture stayed on the screen until their

response. 40 previously presented ("Old") pictures for each set size and 120 new pictures were tested in a pseudo-random order. Of note, a picture that was tested during the object encoding task was never tested in this task.

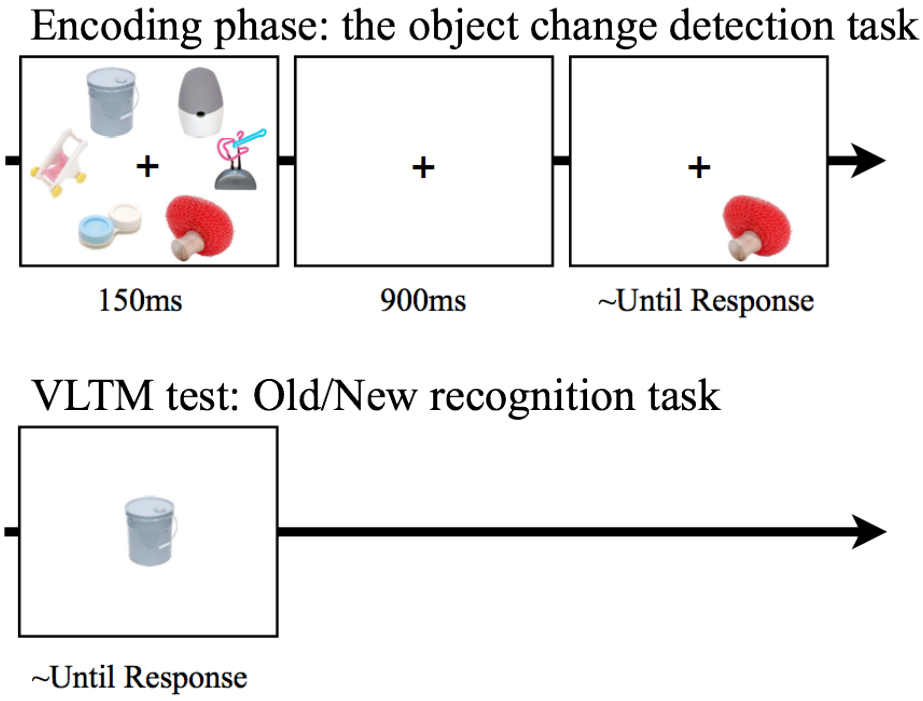

Figure 2. The schematic of Experiment 1a and 1b
The top figure shows the schematic of the encoding phase. In this phase, participants performed an object change detection task. The bottom figure shows the schematic of the long term memory test. In this test, participants judged if the picture presented was presented anytime or anywhere during the encoding phase.

Result

1. VSTM task

First of all, individuals' performance on a VSTM task was converted to VSTM capacity estimate for each set size (K4 for set size 4 and K8 for set size 8) using a standard formula (Cowan 2001). K4 and K8 were averaged to compute a single metric for individuals' VSTM capacity estimates (Kcolor). The mean Kcolor score was 2.6 (S.E.

= .17) for Exp1a, and it was 2.7 (S.E. = .14) for Exp 1b. Based on individuals' Kcolor scores, individuals were divided , by a median split, into high K (mean K = 3.4, S.E. = .14 for Exp 1.a, and mean K = 3.3, S.E. = .12 for Exp 1.b) and low K (mean K = 1.93, S.E. = .13 for Exp 1.a, and mean K = 2.1, S.E. = .11 for Exp 1.b) groups.

2. VLTM encoding phase

In the encoding phase, the change detection accuracy for each set size was again converted to the VSTM capacity estimate. The capacity estimate for each set size was K2 = 1.7 (S.E. = .04), K4 = 2.1 (S.E. = .18), and K6 = 2.1 (S.E. = .17) for Exp 1a, and K2 = 1.7, K4 = 2.1, and K6 = 1.7 for Exp 1b (Figure 3). The results were analyzed by a repeated-measures ANOVA with three factors (instruction x VSTM capacity x set size). As expected, there was a strong set size effect ($F = 7.4$, $p < .01$). In other words, the K estimates increased from set size 2 to 4 and stopped increasing thereafter (as supported by both significant linear ($F = 5.4$, $p < .03$) and quadratic ($F = 9.4$, $p < .01$) effects). There also was a strong main effect of VSTM capacity ($F = 14$, $p < .001$), that high capacity individuals performed better than low capacity individuals. Furthermore, there was a significant interaction between VSTM capacity and the set size ($F = 3.7$, $p < .05$), suggesting that the difference in K estimates for high and low capacity groups increased as a function of set size (as supported by a significant linear effect ($F = 7.1$, $p = .01$)). Simple t-tests revealed that high and low capacity individuals did not significantly differ in performance for set size 2 ($p > .05$) , but they did in higher set sizes ($ps < .01$). There was no main effect of instruction ($F = 2.0$, $p > .1$).

3. Old/New judgment task

Here we measured individuals' corrected recognition performance (Pr = hit rate - false alarm) for each set size. The results were analyzed by a repeated-measures ANOVA with three factors (instruction x VSTM capacity x set size) (Figure 3). First of all, there was a strong set size effect ($F = 24$. $p < .001$). In other words, Pr scores decreased from set size 2 to 4 and stopped decreasing thereafter (as supported by both significant linear ($F = 45$, $p < .001$) and quadratic ($F = 6.1$, $p < .03$) effects). Interestingly, there was a strong main effect of VSTM capacity ($F = 8.9$, $p < .01$), showing that high capacity individuals performed better than low capacity individuals. Furthermore, there was a strong interaction between VSTM capacity and the set size ($F = 6.0$, $p < .01$), suggesting that the difference in Pr scores between high and low capacity groups increased as a function of set size (as supported by a strong linear effect ($F = 13$, $p = .001$)). In fact, simple t-tests revealed that high and low capacity groups did not differ in performance for set size 2 ($p > .5$), but they did in higher set sizes (ps $< .05$). This effect was also supported by the correlation analyses that revealed strong positive relationship between VSTM capacity and Pr scores only in the higher set sizes (rs $< .2$, n.s. for set size 2, but rs $> .43$, ps $< .03$ for set size 6). Thus, the Pr scores perfectly mirrored the change detection performance during the encoding phase. These results strongly confirmed our hypothesis that VSTM capacity determines the bottleneck of information transfer into VLTM.

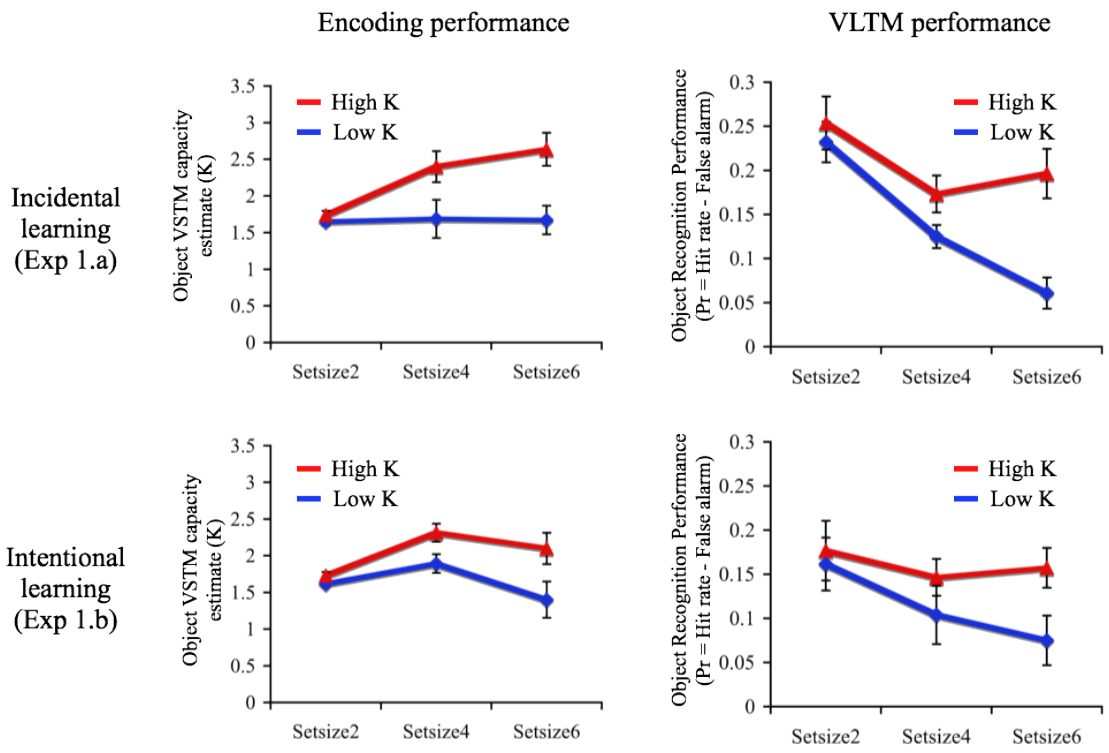

Figure 3. The results of Experiment 1a and 1b.
The top row shows the result of Experiment 1a, and the bottom shows that of Experiment 1b. The left panels show the change detection performance of high and low capacity (K) groups across set sizes. The right panels show the recognition performance of high and low capacity (K) groups across set sizes.

Discussion

In Experiment 1a and 1b, we tested the first and the most basic corollary of the VSTM involvement in LTM encoding. That is, more VSTM representations lead to encoding of more VLTM. Here, using an individual differences approach, we found that individuals with high VSTM capacity estimates were able to encode more objects into VLTM than those with low VSTM capacity estimates. Critically, this relationship was only observed when the number of objects to remember saturated individuals' VSTM

capacity (i.e. set size 6). This adds a very important specificity to the relationship since it suggests that the correlation was not there because high VSTM capacity individuals have better memory in general. Rather, the relationship was driven by the intrinsic role of VSTM capacity serving to determine the amount of information that can be encoded into VLTM at a given time without regard to their intention to learn.

Experiment 2a and 2b: VSTM capacity dictates relational VLTM encoding

In experiments so far, we have investigated the functional role of VSTM capacity in VLTM encoding of independent objects (e.g. I have seen a bucket but not a ball). However, some visual information is evaluated and memorized in relation to other information. For instance, imagine that you are learning a map. To learn a map, you have to encode not only the individual components of the map, but also the interrelations amongst the components (i.e. where was the hospital in relation to my house). Some have argued that relational memory has a specific reliance on the hippocampus and related MTL regions over and above the independent memory.

To extend our finding to arguably different types of memory, we investigated the role of VSTM capacity in creating spatial VLTM. The experimental design was very similar to Experiment 1. After measuring individuals VSTM capacity, participants proceeded to the encoding phase followed by a VLTM recognition test. Here, we chose arrays of colored squares as the stimuli to encode because, unlike pictures of real objects, each array is nearly identical in terms of their components (i.e. a selection of squares from 9 possible colors), but the difference is determined by the relative positions of the squares (i.e. where is the red square in relation to the blue square?). Therefore, to perform

well on the later VLTM test, it is critical to have encoded the relational information of the squares. Here, the prediction is as follows. If VSTM capacity also determines the amount of information encoded to relational VLTM, individuals VSTM capacity should predict VLTM performance only when their VSTM is overloaded. Similarly to the previous experiments, we ran two versions of the same studies to test both incidental (Experiment 2a) and intentional (Experiment 2b) learning.

Participants

After signing the consent form approved by the IRB, 51 students at the University of Oregon (27 for Experiment 2a, and 24 for Experiment 2b) with normal (or corrected to normal) vision participated for the introductory psychology course credits.

Procedure

1. VSTM task

The task was identical to the ones used in the previous experiments.

2. Encoding phase

After the VSTM task, participants performed a color change detection task. The task was identical to the VSTM task except for the following changes. First, 30 different spatial layouts were created for each set size 4 and 8. To avoid high similarity amongst spatial layouts for set size 4, the layouts for set size 4 arrays were hand-crafted. Then, color values were randomly assigned from the 9-color set without replacement within each array. Participants performed the change detection task on these arrays for 15 blocks

within each of which each array was presented 2 times in a pseudo-random order. Therefore by the end of block 10, each array was exposed 30 times. Importantly, the tested location for each array was randomly determined at every exposure. After block 10, to estimate the baseline change detection performance for never-exposed arrays, participants performed an extra block of the change detection task (60 trials each for set size 4 and 8) in which memory arrays were composed of the repeated arrays and the same number of newly created arrays that were never repeated.

3. VLTM test phase

After the encoding phase, participants performed the VLTM recognition task. In this task, participants were presented with one spatial array of colored squares at a time, and they were asked to judge, by a button press, if it was an array that was presented during the encoding phase. The array stayed on the screen until response. 30 previously presented ("Old") arrays for each set size and 30 new arrays for each set size were tested in a pseudo-random order.

Results

1. VSTM task

Individuals' VSTM capacity score (K) was calculated as the average of K estimate for set size 4 (mean K4 = 2.6, S.E. =.11 for Exp 2a, and mean K4 = 2.6, S.E = .13 for Exp 2b) and set size 8 (mean K8 = 2.1, S.E. =.20 for Exp 2a, and mean K4 = 2.5, S.E = .27 for Exp 2b). This resulted in the mean K score of 2.3 (S.E. = .13) and 2.5(S.E = .17) for Experiment 2a and 2b, respectively. The difference in the K scores between

experiments did not reach the statistical significance ($p > .2$). For each experiment, individuals were divided into high (mean K = 2.9 and 3.3 for Exp 2a and 2b) and low K (mean K = 1.8 and 1.8 for Exp 2a and 2b) groups by a median split.

2.VLTM encoding phase

For both experiments, individuals were presented with each memory array 30 times across the span of each experiment. To test the learning effect on change detection performance, we tested if there was an improvement in performance over time. A repeated-measures ANOVA with 3 factors (instruction x set size x repetition) revealed no interpretable effect of repetition ($Fs < 1$, n.s.). In other words, the capacity estimates remained constant across repetitions for both set sizes in both experiments. Furthermore, the comparison of K scores for the repeated arrays and new arrays in the last block of encoding phase did not reveal a significant difference (Kold = 2.1 and Knew = 2.2, n.s., for Experiment 2a, and Kold = 2.7 and Knew = 2.6, n.s., for Experiment2b) (Figure 4). A strong correlation between Kold and Knew ($rs > .7$ $ps < .001$) revealed that the individual differences were also preserved even after repeated exposures to the arrays. This is consistent with previous observation by Olson and Jiang (2005).

To estimate the amount of information maintained in VSTM during the encoding phase, the K scores for each set size were averaged across blocks. A repeated-measures ANOVA with 2 factors (set size x VSTM capacity) revealed the following. Not surprisingly, there was a main effect of VSTM capacity that high capacity individuals performed better ($F = 30$, $p < .001$). Further there was a main effect of set size that K scores were higher for set size 4 than set size 8 ($F = 17$, $p < .001$). Importantly, this effect

was largely driven by the VSTM capacity x set size interaction ($F = 19$, $p < .001$) that K score differences between high and low capacity groups magnified in set size 8. Taken together, these findings proposed a set of straightforward and testable predictions. First, there should be a main effect of VSTM capacity on VLTM performance. In other words, high capacity individuals should perform better on the VLTM task. More importantly, the difference should be largely driven by the VSTM capacity X set size interaction. In other words, the capacity related differences in VLTM performance should be magnified for set size 8 arrays.

3. Old/New judgment task.

As in Experiment1, we focused on the corrected recognition performance (Pr = hit rate - false alarm). A repeated-measures ANOVA with 3 factors (instruction x VSTM capacity x set size) revealed the following results (Figure 4). First, there was a main effect of set size ($F = 102$, $p < .001$) that Pr scores for set size 4 arrays were larger than that for set size 8 arrays. Also, as predicted, there was a main effect of VSTM capacity ($F = 11$, $p < .01$) showing that high capacity individuals showed larger Pr scores. More importantly, there was a VSTM capacity x set size interaction ($F = 4.6$, $p < .05$) revealing that the differences in Pr scores between high and low capacity individuals increased as a function of set size. Correlational analyses further buttressed the observation: individuals' K scores did not significantly correlate with Pr scores for set size 4 ($rs < .28$, n.s.) but they did with for set size 8 ($rs > .59$, $p < .01$).

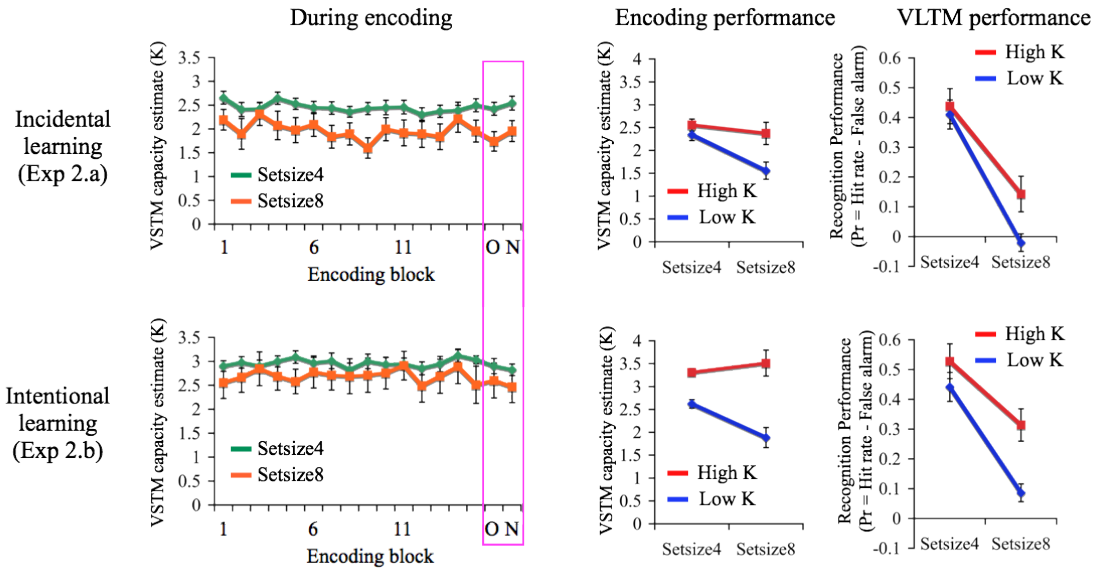

Figure 4. The results of Experiment 2a and 2b.
The top row shows the result of Experiment 2a, and the bottom shows that of Experiment 2b. The left panels show the change detection performance of high and low capacity (K) groups for set size 4 and 8 across the encoding blocks. The middle panels show the mean VSTM capacity estimate for each set size across the encoding blocks. The right panels show the recognition performance of high and low capacity (K) groups for each set size.

Discussion

In Experiment 2a and 2b, we sought to generalize the findings from Experiment 1a and 1b for the encoding of relational VLTM. Here, we found that VSTM capacity determined the relational VLTM performance only when individuals' VSTM were overloaded. The finding was consistent regardless of participants' awareness about the VLTM test. Together with Experiment 1a and 1b, the results suggested that VSTM plays a crucial role in VLTM encoding by imposing a bottleneck for information transfer into the secondary memory system, regardless of the type of information (i.e. object LTM or relational LTM) and the subjects' intention for learning (i.e. incidental learning or intentional learning).

In experiments so far, we have tested the first and the most important corollary of our prediction. That is, VSTM is involved in encoding of VLTM by regulating the information flow with its capacity limit. In all the experiments, our individual differences approach successfully supported the account by showing that strong positive correlations between individuals' VSTM capacity and VLTM performance is only observed when items to remember saturated individuals' VSTM capacity. Metaphorically, it is as if VSTM capacity determines the "bandwidth" of information transfer into VLTM. To further test our insight, we focused on another corollary that captures the nature of the "bandwidth" more directly. More precisely, the "bandwidth" of information transfer determines the speed of information transfer. For example, in computer networking, the size of the bandwidth determines how quickly a given amount of information is transferred to the destination. Thus, in Experiment 3, we attempted to examine this corollary by manipulating the number of opportunities for individuals to encode the information into their VSTM. The prediction was very straightforward. If VSTM capacity determines the "bandwidth", those with high capacity should encode the information at a quicker rate, thus needing less opportunities to represent them in VSTM, compared to those with low capacity.

Experiment 3

In Experiment 3, the procedure was the same as in Experiment 2b except for the encoding phase. After measuring individuals' VSTM capacity, individuals went through

the encoding phase during which they were exposed to 60 different set size 8 arrays. Each third of the arrays were repeated 10, 20 or 30 times across the course of the encoding phase. To demonstrate that the " bandwidth" effect of VSTM capacity is not specific to the encoding phase with a change detection task, we imposed a different encoding task. Here, participants were presented with an array for 150ms, and they simply had to indicate if they have seen the array during the experiment or not. If VSTM capacity is the bottleneck for acquiring the visual representation irrespective of the concurrent task, we should be able to observe a strong positive relationship between individuals' VSTM capacity and the consequent VLTM performances. More importantly, the capacity-related differences in VLTM performances should increase as a function of the number of repetitions.

Participants

After signing the consent form approved by IRB, 29 students with normal (or corrected to normal) vision at the University of Oregon participated for the introductory psychology course credits.

Procedure

1. VSTM task

The task was identical to the ones used in the previous experiments.

2. Encoding phase

After the VSTM task, participants were exposed to 60 different arrays of 8 colored squares. The arrays were presented for 150ms at a time, and each third of arrays was presented 10, 20 , or 30 times in a pseudo-random order. After each exposure, to keep participants focused on the stimulus presentation, they were asked to simply judge if they have already seen the array during the encoding phase.

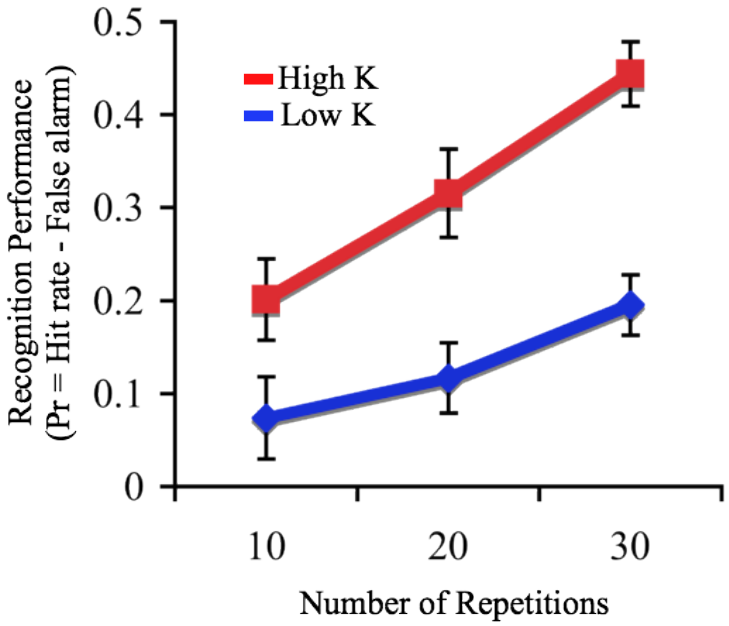

Figure 5. The results of Experiment 3.
The figure shows the recognition performance for high and low VWTM capacity (K) groups as a function of the number of repetitions of encounters to memory arrays during the encoding phase.

3. VLTM test phase

The VLTM recognition task was identical to the one used in Experiment 2a and 2b.

Results

1. VSTM task

Individuals' VSTM capacity score (K) was calculated as the average K estimate

for set size 4 (mean K4 = 2.8, S.E. =.10) and set size 8 (mean K8 = 2.5, S.E. =.21). This resulted in the mean K score of 2.7 (S.E. = .14). Then, individuals were divided into high (mean K = 3.3) and low K (mean K = 2.2) groups by a median split.

2. Old/New judgment task.

We focused on the corrected recognition performance (Pr = hit rate - false alarm). A repeated-measures ANOVA with 2 factors (VSTM capacity x the number of repetitions) revealed the following. First, there was a significant linear effect of the number of repetitions ($F = 47$, $p < .001$) (Figure 5). In other words, the Pr scores improved monotonically as a function of the number of repetition (Pr = .13, .20, .30 for 10 repetitions (Rep10), 20 repetitions (Rep20), and 30 repetitions (Rep30), respectively). Furthermore, there was a main effect of VSTM capacity ($F = 20$, $p <.001$) showing that high K group performed better than low K group. More importantly, there was a significant interaction between VSTM capacity and the number of repetitions ($F = 5.4$, $p < .03$), such that high K group showed a steeper increase in Pr as the function of the number of repetitions. This is consistent with our hypothesis that those with higher VSTM capacity acquire VLTM more quickly than those with lower VSTM capacity. To better characterize the difference in VLTM acquisition rate, we calculated the differences between Pr scores for 30 repetitions and 10 repetitions, and divided them by 20. This is a measure of a VLTM acquisition slope (i.e. how much VLTM is acquired for a given exposure), and we found a significant positive correlation between the VLTM acquisition slope and individuals' VSTM capacity ($r = .4$, $p = .03$).

Discussion

In Experiment 3, we attempted to test another corollary of the "bandwidth" account of VSTM involvement in VLTM encoding. More precisely, those with a larger VSTM capacity acquire the VLTM more quickly than those with a smaller capacity, and the results confirmed the hypothesis. High capacity individuals showed a significantly steeper acquisition slope than low capacity individuals, and this suggests that high capacity individuals needed a fewer number of opportunities to represent the information in VSTM so that they can form the VLTM representations. We were also able to replicate the relationship between VSTM capacity and VLTM performance without imposing a change detection task during the encoding phase. This clearly demonstrates that the relationship was not induced by the specific experimental context due to the demand of a change detection task, but rather, it is generalizable to different learning contexts.

THE LOCUS OF THE "BANDWIDTH" IN VSTM PROCESSES

Across all the experiments, we clearly and consistently observed that VSTM capacity determined the bandwidth of information transfer into VLTM. One thing, however, that is still unclear is which VSTM processes create VLTM representations. To be more specific, we know that more exposures to a given stimulus during the encoding phase increase VLTM performance. At the same time, we know that the stimulus undergoes arguably dissociable VSTM processes at every exposure. For example, first, the stimulus has to be consolidated in VSTM, and then it has to be maintained across the retention interval. At last, its VSTM representation contributes to the response selection

for the assigned task (e.g. change detection task). At this point, it is uncertain which VSTM processes are responsible for VLTM encoding.

For instance, some researchers have theorized that what makes VSTM important for VLTM encoding is the act of maintenance. In other words, VSTM serves as the incubator for information to become a VLTM representation. Although this view has received both support and criticism, it is entirely plausible that the VSTM maintenance gave rise to the relationship we observed in our experiments.

Another line of research points to the importance of the test. Studies on learning have consistently found the positive effect of taking tests on memory of the studied materials (Roediger, III and Karpicke 2006a, 2006b). In our experimental designs so far, VSTM representations of stimuli were always tested at every exposure during the encoding phase, and thus it is also plausible that the improved VLTM performance for the stimuli with multiple exposures can be attributed to the multiple experiences of taking tests. Thus, in the next experiments, we decided to manipulate each VSTM processes to directly test the role of each on VLTM encoding.

Experiment 4a: VSTM maintenance does not incubate VLTM representations

To evaluate the effect of VSTM maintenance as a VLTM incubator, we directly manipulated the duration of VSTM maintenance. After measuring individuals VSTM capacity, participants performed an object VSTM task as the encoding task in which, participants were presented with 2 pictures of real objects (c.f. Experiment 1a and b) to remember across a retention interval. Here, we orthogonally manipulated the number of exposures and the total duration of VSTM maintenance. A quarter of the objects were

presented once and retained over 1.5 second of the retention interval (base). Another quarter of the objects were presented three times across the entire encoding phase, and they were retained over 1.5 second of the retention interval each time (base*3). Based on the previous findings, the VLTM performance for the objects in the base*3 condition should be better than that for the objects in the base condition, and this improvement in performance was what we attempted to account for by orthogonally manipulating each VSTM process.

In one of the critical conditions, one quarter of the objects were presented only once and were retained over 4.5 second of the retention interval (long). If VSTM incubation is the cognitive mechanism that underpins the VSTM involvement in VLTM encoding, the VLTM performance for the objects in this long condition should be equally good as that for the objects in the base*3 condition. In the other critical condition, the last quarter of the objects were presented 3 times during the entire encoding task, and they were retained for .5 second for each retention interval (short*3). If the incubator hypothesis is correct, the VLTM performance for these objects should be as bad as that for the objects in the base condition simply because the total duration of VSTM maintenance is equal to that of the base condition.

Another orthogonal variable that we introduced was the type of test. In all of the experiments, during the encoding phase, participants had to make a decision regarding the stimuli that they were holding in their VSTM (i.e. change detection or old/new judgment task). Different lines of research have shown the positive effect of test on learning (i.e. LTM encoding) and from this perspective, it is also plausible that the observed link between VSTM capacity and VLTM performance might be mediated by

the effect of the test itself. To test this hypothesis, we manipulated the responses during the encoding phase. In one half of the trials in all conditions, one object was presented at the center of the screen after the retention interval, and participants were asked to judge if it was one of the objects originally presented (VSTM test). On the other half of the trials, either "z" or "/" was presented at the center of the screen, and participants were asked to hit the presented key on the keyboard (no test). If the experience of the test was mediating the link between VSTM and VLTM, the VLTM performance for the objects presented in the VSTM test condition should be significantly better that that for the objects presented in the "z or /" test condition.

Participants

After signing the consent form approved by IRB, 23 students with normal (or corrected to normal) vision at the University of Oregon participated for the introductory psychology course credits.

Procedure

1. VSTM task

To ascertain that the samples were drawn from the same distribution in terms of their VSTM capacity, we first run the standard change detection task. The task was identical to the ones used in the previous experiments.

2. Encoding phase

After the VSTM task, participants performed the modified version of the object

change detection task used in Experiment 1a and 1b (Figure 6 A). In this task, every trial presented 2 pictures of real objects for 150ms, and participants were asked to remember them across the retention interval. In a baseline condition (base), the retention interval was 1.5 seconds long, and the pictures were presented only once throughout the encoding phase. In the base*3 condition, each trial had a 1.5 second long retention interval, but each trial was encountered 3 times over the course of the experiment to ensure each picture in this condition was shown 3 times. In the long condition, the retention interval was three times longer (4.5 seconds) than that of the base condition to equate the total duration of the retention interval with the base*3 condition. In the short condition, the retention interval was a third in duration (.5 second) in comparison to the base condition, but each trial was encountered 3 times across the experiment to equate the total retention interval with the base condition.

Orthogonal to the retention interval manipulation, the type of the test was also manipulated. In one half of all the conditions, the retention interval was followed by a typical VSTM test, in which, participants had to judge if the picture presented at the center was identical to the pictures presented in the preceding memory array. The change frequency was 50% to control for any response bias. On the other trials, the retention interval was followed by the presentation of "z" or "/" at the center of the screen. Here, participants were asked to simply press the key presented.

The number of trials run for each condition was 60 for the base and the long condition, and 180 for the base*3 and the short condition to ensure that the same number of pictures would be tested in the following VLTM test (Importantly in VSTM test condition, the same picture was tested across multiple exposures in order to leave the to-

be-tested stimuli for the VLTM recognition test untested).

3. VLTM test phase

The VLTM recognition test was identical to the one used in Experiment 1a and 1b. 30 "old" pictures for each condition (30 x 4 (= base, base*3, long and short) x 2 (VSTM test and "z or /" test) = 240 pictures in total) and 60 new pictures were presented during the test. Of note, none of the pictures used in the VSTM test were presented.

Result

1. VSTM task

The VSTM task was implemented just to ascertain that this sample population had roughly the same characteristics as the ones that participated in the other experiments. Individuals' VSTM capacity score (K) was calculated as the average of K estimate for set size 4 (mean K4 = 3.1, S.E. =.09) and set size 8 (mean K8 = 2.5, S.E. =.26). This resulted in the mean K score of 2.8 (S.E. = .15). The result confirmed that the sample population was equivalent to the samples used in the other experiments.

2. VLTM encoding phase

The performance on the encoding task was analyzed for each condition. For the "z or /" test conditions, not surprisingly, the accuracy was at ceiling across all conditions (accuracies > .98 for base, base*3, short, and long). For the VSTM test conditions, the only condition that was significantly worse in accuracy than others was the long condition (accuracy = .83 for long compared to .91, 92, and .94 for base, base*3 and

short, ps < .03). This suggested that the amount of VSTM representations retained across the long retention interval was detectably less than that retained across shorter retention intervals. A K-transformation revealed a small difference in the number objects held across the retention interval for each condition (K = 1.6, 1,7, 1.8, and 1.4 for base, base*3, short*3, and long conditions, respectively).

3. VLTM test

First of all, the effect of the test was analyzed by averaging across all base, base*3, short and long conditions. Markedly, there was no difference in LTM performance based on the type of the test (Pr = .21 for the "z or /" test and Pr = .21 for the VSTM test conditions) (Figure 6 B). This clearly demonstrated that the link between VSTM capacity and VLTM was not mediated by the experience of the test (n.s.). Next, the effect of maintenance was analyzed. Given the null effect of the test types, the Pr scores were averaged across the test types for the later analyses. A repeated-measures ANOVA revealed that there was a significant effect of learning conditions ($F = 29$, $p < .001$) (Figure 6 C). To further characterize the results, a series of t-test were conducted. First, as expected, the Pr scores for the base*3 conditions were significantly better than the Pr scores for the base condition (Pr = .29 for base*3 and Pr = .15 for base, $p < .001$). Strikingly, the Pr score for the long condition (Pr = .16) was statistically equivalent to that for the base ($p > .7$) and significantly lower than that for the base*3 ($p < .001$). On the other hand, the Pr score for the short*3 (Pr = .26) condition was significantly better than that for the base ($p > .001$) and statistically equivalent to that for the base*3 ($p > .05$). These results clearly point to the fact that longer VSTM maintenance on its own did not

positively impact the VLTM performance.

Discussion

In Experiment 4, we directly tested several hypotheses that can account for the link between VSTM capacity and VLTM encoding, and we obtained clear results refuting two of them. First, we observed no evidence for the effect of the VSTM test on VLTM encoding. More precisely, the VLTM performance for the objects that were associated with the VSTM tests was no better than that for the objects that were not. This demonstrates that the involvement of VSTM in VLTM encoding was not through the experience of the VSTM test.

We also found no evidence for the VSTM incubation hypothesis. Surprisingly, the VSTM maintenance duration per se had negligible impact on VLTM performance. More precisely, retaining VSTM representations for a 3 times longer period of time (4.5 seconds vs 1.5 seconds) did not improve VLTM encoding of the representation. It was rather the number of opportunities for VSTM maintenance that had a significant impact on VLTM encoding. Increasing the number of VSTM maintenance while keeping the total VSTM maintenance duration significantly improved the VLTM performance. Taken together, the observed involvement of VSTM was neither mediated by the duration of maintenance nor the experience of VSTM test, but by the number of opportunities for VSTM maintenance. These results are highly consistent with both behavioral and neurophysiological findings that highlighted the disproportional importance of the early stages of VSTM maintenance in VLTM encoding (Naveh-Benjamin and Jonides 1984b; Ranganath et al., 2006).

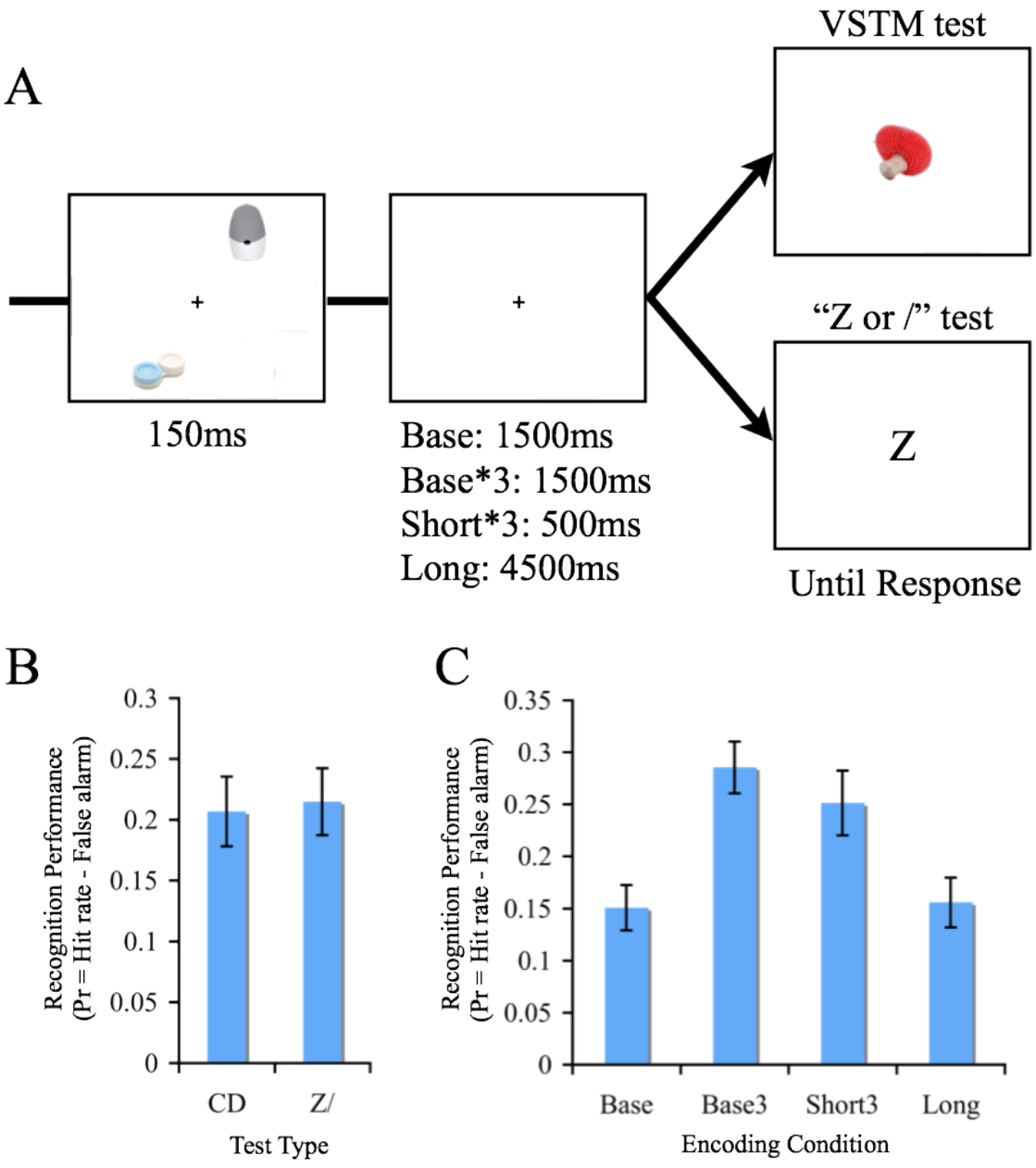

Figure 6. The schematic and the results of Experiment 4a.
Panel A shows the schematic of the encoding phase. Panel B shows the recognition performance for two test types. Panel C shows the recognition performance for four encoding conditions.

Experiment 4b: VSTM consolidation dictates VLTM encoding

Experiment 4a suggested the importance of the early stage of VSTM maintenance (i.e. the first 500 ms of VSTM maintenance) in VLTM encoding. From VSTM literature, we know that this is the exact time window when visual representations become consolidated in VSTM (Vogel, Woodman, and Luck 2006). Therefore, in Experiment 4b, we experimentally manipulated VSTM consolidation to investigate its effect on VLTM encoding. After measuring individuals VSTM capacity, we administered an object encoding phase. In this phase, participants were presented with 3 pictures of real objects to remember across a retention interval. To manipulate the VSTM consolidation of the stimuli, we presented masks at various ISIs from the offset of the stimuli. It is known that post-stimulus masks disrupt the consolidation of VSTM representations at various degrees depending on the stimuli to mask ISIs. To be more specific, it has been found that the shorter the ISI, the more disruption to VSTM consolidation. If VSTM consolidation is the determinant factor for VLTM encoding, we should expect that the masking effect on VSTM consolidation directly translates to VLTM encoding.

Participants

After signing the consent form approved by IRB, 26 students with normal (or corrected to normal) vision at the University of Oregon participated for the introductory psychology course credits.

Procedure

1. VSTM task

To ascertain that the samples were drawn from the same distribution in terms of VSTM capacity, we first run the standard change detection task. The task was identical to the ones used in the previous experiments.

2. Encoding phase

After the VSTM task, participants performed the modified version of the object change detection task used in Experiment 1a and 1b (Figure 7A). In this task, every trial presented 3 pictures of real objects for 150ms, and participants were asked to remember them across the retention interval that was followed by the same VSTM test as in Experiment 4a. In 200 out of 280 trials, short rapid serial presentations of mask stimuli (50 ms each for 3 stimuli) were presented at each memory item location during the retention interval at 0ms, 100ms, 300ms, 600ms or 1500ms after the offset of the memory array with equal probabilities. The mask stimuli were created by overlaying multiple unused pictures from the picture set. The duration of the retention interval was 1500ms for 0ms, 100ms, 300ms, and 600ms mask conditions, but for 1500ms mask condition, it was set to 2400ms to give enough temporal separation between the mask presentation and the test stimulus.

In the rest of trials, no mask was presented during the retention interval. To have an equal duration of the retention interval, a half of the trials had a 1500ms long retention interval, and the other half had a 2400ms long interval.

3. VLTM test phase

The VLTM recognition test was identical to the one used in Experiment 1a and 1b. 40 "old" pictures for each condition (280 total) and 40 new pictures were presented during the test. Of note, none of the pictures used in the VSTM test were presented.

Result

1. VSTM task

The VSTM task was implemented just to ascertain that the sample population has roughly the same characteristics as the ones that participated in the other experiments. Individuals' VSTM capacity score (K) was calculated as the average of K estimate for set size 4 (mean K4 = 2.8, S.E. =.08) and set size 8 (mean K8 = 2.8, S.E. =.19). This resulted in the mean K score of 2.8 (S.E. = .11). This result confirmed that the sample population was equivalent to the samples used in the other experiments.

2. The effect of masking on VSTM consolidation

First of all, the effect of masking was analyzed for VSTM consolidation. When no mask was presented, the mean change detection accuracy was .78 (S.E. = .01). For mask conditions, a repeated-measures ANOVA revealed significant linear ($F = 29$, $p < .001$) and quadratic ($F = 9.2$, $p < .01$) effects. In other words, the change detection accuracy showed a monotonic increase as a function of ISI from 0ms to 600ms and it stabilized (mean accuracy = .66, .73, .74, .78, and .76 for 0ms, 100ms, 300ms, 600ms, and 1500ms ISIs, respectively). T-tests revealed that the change detection performance was no longer different after the 600ms ISI (ps > .7), suggesting that the VSTM consolidation was fully

complete by 600ms after the offset of the memory array.

3. The effect of masking on VLTM performance

VLTM performance (= Pr) was analyzed as a function of the masking ISIs (Figure 7B). First, the effect of masking was examined. To equate the VSTM performance, the Pr for the no mask condition was compared to the average Pr scores for the 600ms and 1500ms ISI conditions. Interestingly, the Pr scores for the masked conditions were significantly better than those for no mask conditions ($p < .05$). This suggests that the presence of the masks encouraged individuals to "refresh" the VSTM representations, and thus led to better VLTM performance (Johnson et al. 2002).

Next, a repeated-measures ANOVA was conducted to examine the effect of masks. Similarly to VSTM performance, it revealed both significant linear ($F = 16$, $p < .001$) and quadratic ($F = 7.6$, $p = .01$) effects of mask ISIs. More precisely, Pr scores showed a monotonic increase as a function of the ISI from 0ms to 600ms and it stabilized thereafter (mean Pr = .1, .17, .16, .20, .17 for 0ms, 100ms, 300ms, 600ms, and 1500ms ISIs, respectively). These results perfectly mirrored the effect of masking on VSTM performance. To further evaluate the effect of the masking ISIs jointly for VSTM and VLTM performance, we created a scatterplot for VSTM and VLTM performance. This revealed a strong positive correlation between VSTM and VLTM performance. In fact, a simple linear trend was sufficient to explain 95 percent of the variance.

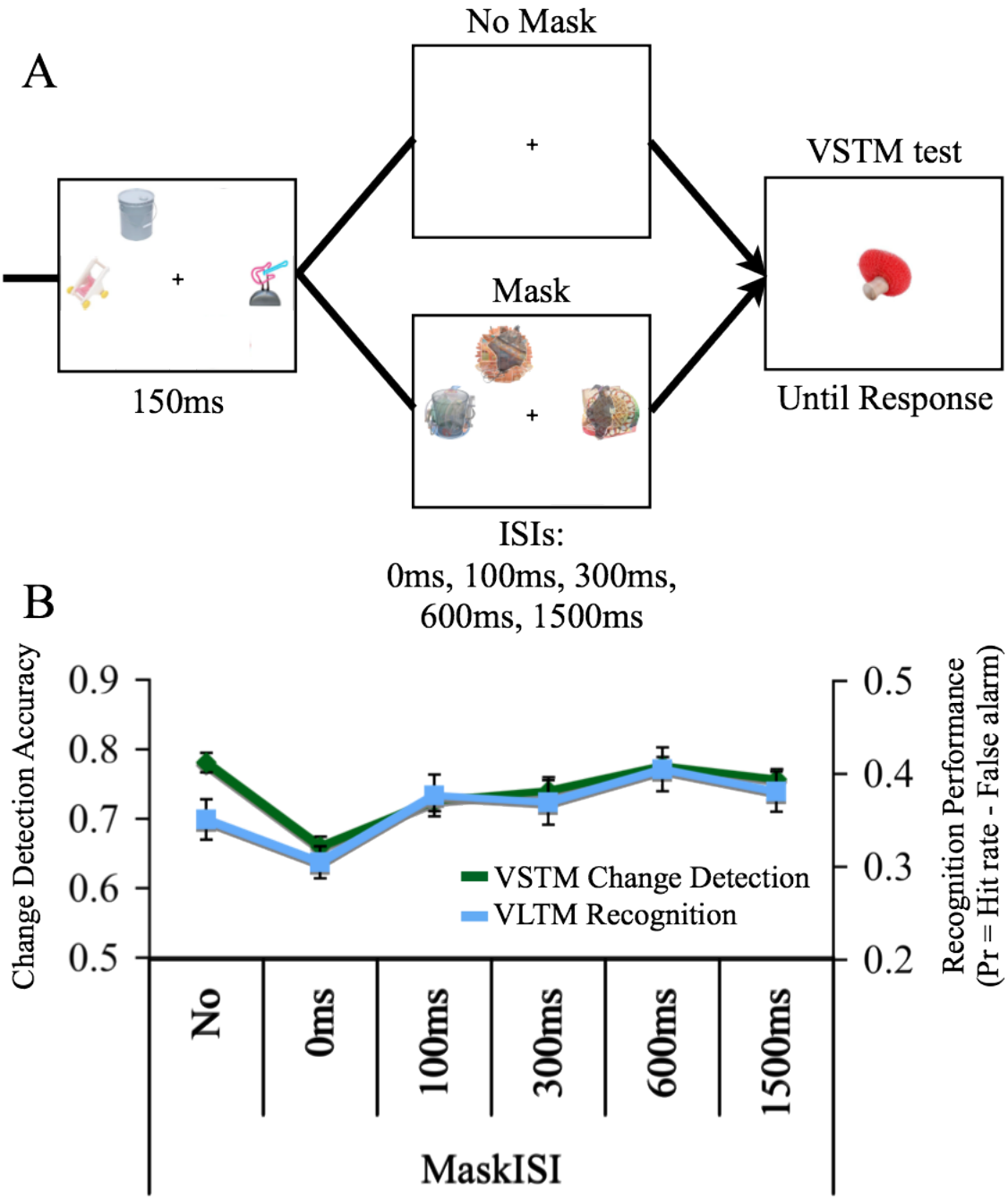

Figure 7. The schematic and the results from Experiment 4b.
Panel A shows the schematic of the encoding phase. Panel B shows the recognition performance for the change detection performance during the encoding and the recognition performance.

Discussion

In Experiment 4b, we directly manipulated the VSTM consolidation to test its impact on VLTM encoding. As predicted, we successfully modulated the VLTM encoding through disrupting VSTM consolidation by masking. In fact, the effect of masking was so transparent that the within-subject fluctuations of VSTM performance were linearly predictive of VLTM performance with r = .97. Taken together with the results from Experiment 4a, in our experimental procedures, it is the VSTM consolidation process that determined the success in VLTM encoding.

ATTENTIONAL CONTROL "THROTTLES THE BANDWIDTH" THROUGH VSTM CAPACITY

In the experiments above, we have taken advantage of inter and intra individual differences in VSTM capacity to explore its direct involvement in VLTM encoding. Findings so far suggest that the amount of information consolidated in VSTM capacity determines the amount of information transferable to VLTM. A traditional interpretation of such findings would be that individuals vary in the physical size of the "bandwidth" (= VSTM capacity). The analogy in computer networking would be that some new (and more functional) networks have broader bandwidth than the older ones. However, an alternative interpretation is that individuals do not differ much in the physical size of the "bandwidth" (= maximum bandwidth, or VSTM capacity), but that they differ in how well they can regulate the information flow in a case of overflow. Again to use computer

networking as a metaphor, imagine two networks with the same maximum bandwidth. Both networks perform equally well when transferring information up to their bandwidth. However, when confronted with more information than they can handle, networks that cannot regulate the information traffic will often suffer from, if not a crash, information congestion, and they will end up transferring junk or less than optimal amount of information. This ability is called "bandwidth throttling", and it could very well be the underlying mechanism that determines the efficiency of information transfer in human memory systems.

Supporting evidence for such an interpretation exists in the VSTM literature. Across multiple paradigms, individuals with low VSTM capacity estimates are known to have impaired attentional control (Vogel, McCollough, and Machizawa 2005; McNab and Klingberg 2008; Fukuda and Vogel 2009, 2011). In other words, they are more disrupted by the presence of distractors, and they cannot help but process them. For example, when individuals are performing a change detection task with a memory array that also contained distractors, electrophysiological signature of VSTM maintenance showed that low capacity individuals cannot help but maintain the distractors in their VSTM, whereas high capacity individuals are able to filter them out of their VSTM (Vogel, McCollough, and Machizawa 2005). Based on such findings, we investigated the VLTM consequences of suboptimal bandwidth throttling in VSTM.

Experiment 5

In this experiment, we borrowed a VSTM filtering task from Vogel, McCollough, and Machizawa (2005). After measuring individuals' VSTM capacity, participants

performed a VSTM filtering task. In this task, participants were first presented with 2 red circles that demarcated the locations where target pictures were going to be presented. Then, two pictures of objects were presented in the demarcated locations. Importantly, in one half of the trials, four distractor pictures were additionally presented outside of the circled locations. Participants were instructed in advance that the only items that can possibly change (therefore be tested) are the two target pictures, and therefore that they should ignore the distractors. After the filtering paradigm, participants performed a surprise VLTM recognition task on both the target and distractor objects. If individuals (we predicted to be low VSTM capacity individuals) failed to filter the distractors (i.e. a failure in bandwidth throttling), they should be left with more distractor VLTM than those who succeeded in bandwidth throttling (we predicted those to be high VSTM capacity individuals).

Participants

After signing the consent form approved by IRB, 26 students with normal (or corrected to normal) vision at the University of Oregon participated for the introductory psychology course credits.

Procedure

1. VSTM task

The task was identical to the ones used in the previous experiments.

2. Encoding phase

After the VSTM task, participants performed the modified version of the object change detection task used in Experiment 1a and 1b (Figure 8A). In this task, each trial started with a 500ms presentation of 2 red circles (radius = 5.32°). These circles served as placeholders for to-be presented target pictures. 200ms later, two target pictures of real objects were presented at the place holder locations, and participants had to remember them over the 1.5 second retention interval. After the retention interval, one of the target pictures was tested by the change detection procedure (see Experiment 1a and 1b). Importantly, in a half of trials, we imposed a situation in which "throttling" bandwidth was critical. Precisely, unlike the other half of trials in which two target pictures were presented alone, (T2D0 condition), we presented 4 task-irrelevant pictures around the target pictures (T2D4 condition). Participants were informed in advance that those task-irrelevant pictures were never tested (in the change detection task), and therefore, they were strongly encouraged to ignore them. Each picture was presented 5 times either constantly as the target or distractor across the entire encoding phase. In the end, participants performed 500 change detection trials.

3. VLTM test phase

The VLTM recognition test was identical to the one used in Experiment 1a and 1b. 50 "old" pictures from for each condition (50 from T2D0 targets, T2D4 targets, and T2D4 distractors) and 50 new pictures were presented during the test. Of note, none of the pictures used in the VSTM test were presented.

Result

1. VSTM performance

Individuals' VSTM capacity score (K) was calculated as the average K estimate for set size 4 (mean K4 = 2.8, S.E. =.10) and set size 8 (mean K8 = 2.3, S.E. =.20). This resulted in the mean K score of 2.5 (S.E. = .13). This result confirmed that this sample population was equivalent to the samples used in the other experiments. Based on the K score, individuals were divided, by median split, into low and high capacity groups (mean K = 2.0 and 3.0 for low and high capacity group respectively).

2. VLTM encoding phase

Individuals' performance was near perfect on T2D0 condition (mean accuracy = .94, S.E. = .01), and they were significantly worse at T2D4 condition (mean accuracy -= .90, S.E. = .02). Not surprisingly, it was the low VSTM capacity individuals who suffered more from the presence of distractors (drop in accuracy = .07, $p < .01$, drop in accuracy = .00, n.s. for low and high capacity group respectively).

3. VLTM test

The corrected recognition performance (Pr = hit rate - false alarm) was compared across the T2D0 targets, T2D4 targets, and T2D4 distractors. First of all, the Pr score for the T2D0 targets was equally good as that for T2D4 targets (the mean Pr = .35 and .35 for T2D0 targets and T2D4 targets respectively, n.s.). Not surprisingly, the Pr score for the T2D4 distractors was significantly worse than those in the other conditions (mean Pr = .08, ps < .01). These results suggest that individuals overall were able to throttle their

bandwidth to selectively (to some extent) encode information to their VLTM (Figure 8B).

Next, the Pr scores were analyzed based on individuals' VSTM capacity. For both target pictures, Pr scores did not differ between low and high capacity groups (the mean Pr for T2D0 target = .35 and .36 for low and high capacity groups, the mean Pr for T2D4 target = .36 and .34 for low and high capacity groups, both n.s.). However, for distractor pictures, it was the low capacity group who showed higher Pr scores (the mean Pr for T2D4 distractor = .13 and .04 for low and high capacity groups, $p < .03$). These results further specified our "bandwidth" theory by showing that it was low capacity individuals that were worse at throttling the bandwidth, and consequently stored "more" junk information in their VLTM.

Discussion

Here, we successfully demonstrated a case in which low VSTM capacity individuals encoded "more" information than high capacity individuals. This was achieved by requiring individuals to "throttle their bandwidth" by introducing distractors. Based on previous literature on individual differences in VSTM capacity, we hypothesized that low VSTM capacity individuals would have difficulty filtering out the task-irrelevant distractors, and therefore encode them into VLTM. The results confirmed our hypothesis. This finding is in stark contrast with the prediction based on the interpretation that individuals with low VSTM capacity have a physically smaller bandwidth, and therefore they encode less information into VLTM in any case than those with high capacity.

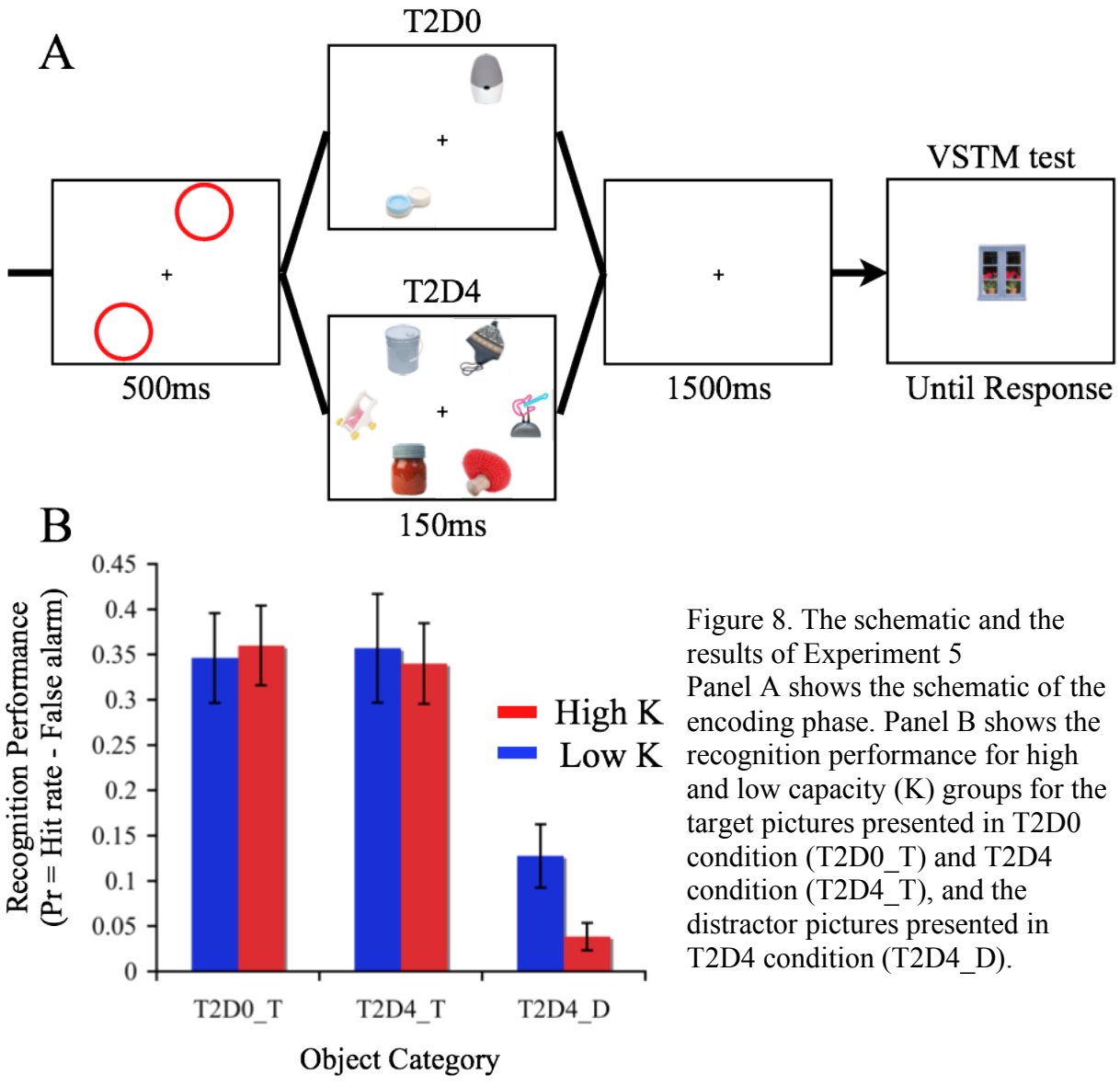

Figure 8. The schematic and the results of Experiment 5
Panel A shows the schematic of the encoding phase. Panel B shows the recognition performance for high and low capacity (K) groups for the target pictures presented in T2D0 condition (T2D0_T) and T2D4 condition (T2D4_T), and the distractor pictures presented in T2D4 condition (T2D4_D).

GENERAL DISCUSSION

Across all the experiments so far, we have attempted to test a very simple and intuitive model of memory. That is, VSTM is directly involved in the encoding of VLTM. Despite its intuitiveness, this view has been questioned for a long time for various reasons. Here, by utilizing inter- and intra- individual differences, we have once

again examined the question, and have consistently found that VSTM is directly involved in VLTM encoding by determining the bandwidth of information transfer of external information into VLTM. Further, it was the ability to attentionally "throttle" the bandwidth that had a fundamental impact on determining the efficiency of VLTM encoding.

Further, we succeeded in conceptually replicating the negative evidence for the involvement of certain aspects of VSTM processes in VLTM encoding. First, we showed that when individuals were presented with sub-capacity objects to remember (i.e. set sizes 4 and below), VSTM capacity did not determine individuals' success on VLTM encoding. In previous research, the primary tasks used to investigate the role of VSTM in VLTM encoding presented items to remember sequentially with 1 item at a time (e.g. running span task). Such a presentation arguably tapped into a different limitation of the memory system than how much information VSTM can maintain at a given time, and thus led to the mixed results in the literature. Second, we showed that it was the VSTM consolidation rather than sheer VSTM maintenance that disproportionately contributed to VLTM encoding. This finding perfectly matches with the initial rebuttal to the modal model of memory and more recent partial support from the dual-stage maintenance models. Taken together, we were able to support the intuitive model of memory by strictly specifying the nature of VSTM involvement in VLTM encoding. That is, once again, VSTM capacity determines the bandwidth of information transfer into VLTM, and individuals' ability to throttle the bandwidth plays a crucial role in VLTM encoding when overloaded with information.

CHAPTER III

VSTM CAPACITY ALSO DETERMINES THE "BANDWIDTH" OF IMPLICIT VLTM ENCODING

INTRODUCTION

In this dissertation, we have focused on memories that are explicitly retrieved (i.e. individuals had to explicitly judge if the presented information is remembered or not). At the same time, we know from the literature that our past experiences can influence our behavior without reaching our explicit awareness. For example, previously seen images can be identified faster than images that were never seen before (i.e. perceptual priming) even when individuals cannot explicitly recognize them. Alternatively, previously encountered items can bias the spontaneous generation of items for the related categories(i.e. conceptual priming). Previous studies have mainly focused on the dissociability of implicit memory from explicit memory, and while many have found a double-dissociation between them in amnesic patients (Milner et al. 1968; Warrington and Weiskrantz 1974; Cohen and Squire 1980; Graf et al. 1984; Moscovitch 1982; Schacter 1985) as well as in normal individuals (Graf et al. 1982; Jacoby and Dallas 1981; Tulving et al. 1982; Blaxton 1989; Roediger, Weldon, and Challis 1989; see Roediger 1990 for review), much less effort has been made to lay out the commonalities between them (Turk-Brown et al. 2006; Daselaar et al. 2006; Reder et al. 2009). If PM serves as the sole gate for SM formation, the implicit memory should also go through this bottleneck. At this point as I briefly reviewed in chapter 1, no direct test of such a hypothesis has been reported, and indirect evidence so far has been ambiguous. Thus, in

the next experiments, we sought to investigate if VSTM capacity also determines the bandwidth for implicit learning.

VSTM CAPACY DICTATES THE ENCODING OF VLTM WITHOUT EXPLICIT CONFIDENCE OF RETRIEVAL

In this experiment, we decided to see if our spatial array paradigm (used in Experiment 2a and 2b) is capable of detecting individuals' memories that are not explicitly retrievable. To do so, we modified the VLTM test procedure. In this version, participants were presented with an old array and a new array side by side, and they were asked to choose the old array. At the same time, participants had to indicate if they were able to pick the array based on their explicitly available memory ("Remembered") or not ("Guessed") (see Voss, Baym, and Paller 2008 and Voss and Paller 2009 for the method). If individuals do have memories that are not explicitly retrievable, they should be better than chance at choosing the old arrays even when they are guessing. Further, if VSTM capacity determines the bandwidth for memories that are not explicitly retrievable, it should be the high capacity individuals that are more accurate at guessing the old arrays.

Experiment 6

Participants

After signing the consent form approved by IRB, 32 students with normal (or corrected to normal) vision at the University of Oregon participated for the introductory psychology course credits.

Procedure

1. VSTM task

The task was identical to the ones used in the previous experiments.

2. Encoding phase

The encoding task was nearly identical to the ones used in Experiment 2a and 2b except for the following. First, we only tested the set size 8 arrays of colored squares. 100 different arrays were created in the same procedures, and each half of the arrays were presented 10 or 20 times across the experiment. Of note, the test item for each array was randomly selected at every exposure. Also, unlike the previous experiments, arrays were presented within a boundary defined by a black square frame at the center of the screen (13.7°x13.7°). This was done to provide a consistent spatial reference for arrays between the encoding task and the recognition task in which two different arrays were presented simultaneously side by side.

3. VLTM test phase

A forced-choice recognition task used in Voss and Paller (2009) was modified (Figure 9A). In this task, two arrays of 8 colored squares, each within the black square frame, were presented side by side on the computer screen. Participants were asked to select one array as the "old" array by a button press ("Z" to pick the left one, and "/" to pick the right one) either based on their explicit retrieval or on a guess when there is no explicit retrieval available. After selecting an array, participants indicated if they

"remembered" seeing the array, or if they had to "guess" by a button press ("R" for remembered, and "G" for guessed). The arrays remained until the second response.

Result

1. VSTM task

Individuals' VSTM capacity score (K) was calculated as the average K estimate for set size 4 (mean K4 = 2.7, S.E. =.09) and set size 8 (mean K8 = 2.6, S.E. =.20). This resulted in the mean K score of 2.7 (S.E. = .14). The result confirmed that the sample population was equivalent to the samples used in the other experiments. Based on the K score, individuals were divided into low and high capacity groups by a median split (mean K = 2.1, 3.2 for low and high capacity group respectively).

2. VLTM task

A repeated-measures ANOVA with 3 factors (VSTM capacity x Retrieval x Repetition) was conducted. Here, we found no effect of repetition (ps > .2) (i.e. recognition performance did not differ in any way with respect to the number of repetition.) Thus, we decided to collapse across the repetition conditions to increase the power of the analyses, and this led to a repeated-measures ANOVA with 2 factors (VSTM capacity x Retrieval). First, the effect of retrieval fidelity ("Remembered" vs "Guessed") was examined, and as predicted, individuals were significantly better at choosing the old arrays when they "remembered" seeing them. ($F = 4.0$, $p = .055$). Importantly, a post-hoc t-test revealed that individuals were significantly better than chance at "guessing" the old array ($p < .01$). Further, there was a main effect of VSTM

capacity that high capacity individuals were more accurate at choosing the old arrays ($F = 11$, $p < .01$). Critically, there was no interaction between VSTM capacity and retrieval fidelity ($F = .58$, $p > .4$), suggesting that high capacity individuals outperformed the low capacity individuals across both retrieval fidelities (Figure 9C). Additionally, correlational analyses revealed that that individuals VSTM capacity was positively correlated with VLTM performances for both fidelities ($rs > .4$ $ps < .03$).

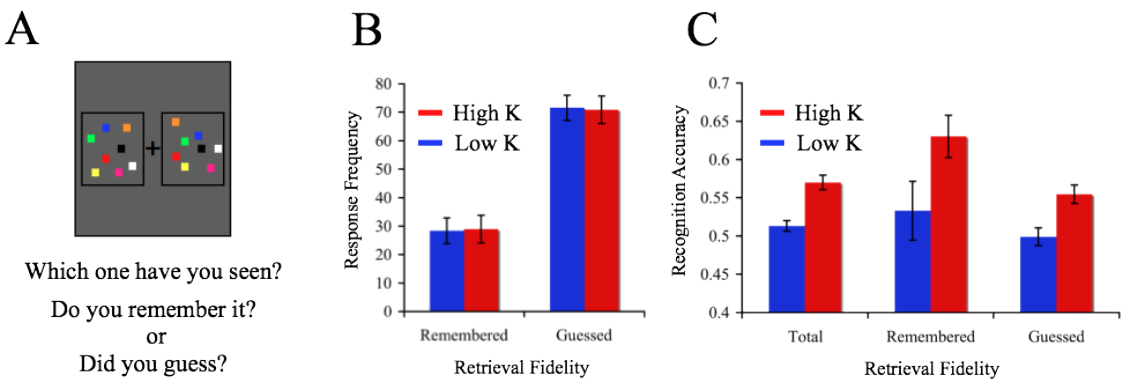

Figure 9. The schematic and the results of Experiment 6
Panel A shows the schematic of the recognition task. Panel B shows the response frequency for high and low capacity (K) individuals during the recognition phase. Panel C shows the recognition accuracy for high and low capacity individuals for total, "remembered", and "guessed" trials.

Discussion

In Experiment 6, we sought to test if VLTM that is not explicitly retrievable is also gated by VSTM. To do so, we modified our relational memory paradigm so that we could separately extract the VLTM performance based on individuals' retrieval fidelities (i.e "Remembered" or "Guessed"). As expected, when memory is explicitly retrieved (i.e. Individuals indicated the old array was "remembered"), individuals were better at specifying the old array than when its memory was not explicitly accessible (i.e.

Individuals “guessed” the old arrays.). However, more importantly, individuals were still better than chance at choosing the old arrays even when they were guessing. These results validated that the memory traces that cannot be explicitly retrieved were measurable with our paradigm. Furthermore, VLTM performance for both “remembered” and “guessed” trials was positively correlated with individuals’ VSTM capacity. These results suggest that, just like the explicit memory, a memory that is not explicitly accessible is acquired through the “bandwidth” set by VSTM capacity.

VSTM CAPACITY DICTATES AN INDIRECT MEMORY EFFECT WITHOUT EXPLICIT ACT OF RETRIEVAL

In Experiment 6, we found positive evidence that a memory that is not explicitly accessible is also encoded through the VSTM bandwidth. One potential problem is , however, that even though we classified the trials based on the retrieval fidelity, participants were “explicitly trying” to retrieve the memory. In the implicit memory literature, another criterion often used to define implicit memory is that participants are not explicitly aware of their act of retrieval. In other words, an implicit memory effect is often measured as the change in performance on a task that does not directly require memory retrieval.

One well-studied indirect memory phenomenon is called contextual cueing. Contextual cueing is an associative learning of spatial configurations within which a target object is presented. Traditionally, it has been studied in the context of visual search task in which participants were asked to identify a target item that is presented with

multiple distractors surrounding it. When participants are performing a visual search task, some configurations of search arrays are repeated multiple times. The typical finding is that participants get faster at performing the search task for the arrays that were repeatedly presented, and this indicates that participants were able to learn the contextual information of the repeated array (i.e. where the target is among distractors). To further support its implicit nature, this effect can be observed despite the lack of explicit knowledge about the repeated arrays (Chun and Jiang 1998, see Chun, 2000 for review).

To incorporate contextual cueing in our relational memory paradigm, we modified the procedure in the following manner. After measuring individuals' VSTM capacity, participants performed more color change detection tasks with repeated memory arrays(encoding phase). Critically, to establish the contextual association, the tested location for each repeated memory array was fixed for every exposure. Consequently, if participants are able to learn the contextual association, their change detection performance should improve for the repeated arrays as a function of the number of repetitions. Furthermore to ensure the "implicitness" of contextual cueing, participants performed a surprise old/new judgment task on memory arrays, and the contextual cueing effect for arrays that participants indicated that they have not seen was evaluated. If implicit learning as measured by contextual cueing effect is also gated by VSTM, the amount and the rate of this learning should depend on individuals' VSTM capacity.

Experiment 7

In this experiment, we modified our spatial array paradigm to incorporate the contextual cueing. After measuring VSTM capacity, participants continued performing

the color change detection task for the encoding phase. During the encoding phase, each memory array was repeated 30 times. Critically, the test item and location was fixed uniquely for each memory array. This manipulation made the learning of the context (i.e. the test item location relative to a memory array) beneficial in performing the change detection task. Further, to increase the effect of contextual cueing, we provided the feedback when participants made mistakes. Here, the measure of the interest was the indirect memory effect on the change detection performance. If the associative learning does happen over repetitions and it implicitly helps the performance, individuals should show improved change detection performance as a function of the number of repetitions. Additionally, if the rate of such a learning is also governed by the VSTM capacity, we should expect a faster, and as a result, a larger improvement in change detection performance for high capacity individuals.

Participants

After signing the consent form approved by the IRB, 29 students with normal (or corrected to normal) vision at the University of Oregon participated for the introductory psychology course credits.

Procedure

1. VSTM task

The task was identical to the ones used in the previous experiments.

2. Encoding phase

The encoding task was nearly identical to the ones used in Experiment 2a and 2b except for the following (Figure 10 A). First, we only tested the set size 8 arrays of colored squares. 16 different arrays were created using the same procedures, and they were presented 30 times across 10 blocks within each of which every array was presented 3 times in a pseudo-random order. Critically, the test item and location for each array was uniquely fixed for every exposure. Also, unlike in the previous experiments, a negative auditory feedback was presented when participants made an error. Both manipulations were included to induce the contextual cueing effect. After the 10th block, participants performed an extra block of the color change detection task on 60 newly created arrays to estimate their baseline performance for the arrays that were neither shown nor repeated.

3. VLTM test phase

The VLTM test was identical to the ones used in Experiment 2a, 2b and 4a. 16 old arrays 16 new arrays were tested.

Result

1. VSTM task

Individuals' VSTM capacity score (K) was calculated as the average K estimate for set size 4 (mean K4 = 2.6, S.E. =.12) and set size 8 (mean K8 = 2.3, S.E. =.21). This resulted in the mean K score of 2.4 (S.E. = .14). This result confirmed that the sample population was equivalent to the samples used in the other experiments. Based on the K score, individuals were divided, by median split, into low and high capacity groups (mean

K = 1.8, 3.0 for low and high capacity group respectively).

2. Contextual cueing

First of all, the accuracy scores for the change detection task were converted to K scores. Then, a repeated-measures ANOVA with 2 factors (VSTM capacity x Repetition) was conducted (Figure 10B). Not surprisingly, there was a significant main effect of VSTM capacity ($F = 16$, $p < .001$) as well as a significant linear trend of the number of repetitions ($F = 40$, $p < .001$). This suggests that individuals were able to learn and utilize the contextual cue to improve their performance. This observation was further buttressed by the comparison of the change detection performances for the repeated arrays and that for the new arrays introduced in the very last block (new block). The comparison started to show a significant difference at block 4 ($K = 3.3$ vs $K = 2.4$ for block 4 and new block, respectively, $p = .01$), and it stayed significant throughout the later blocks ($K = 4.5$ vs $K = 2.4$ for block 10 and new block, respectively, $p < .00001$).

More interestingly, there was a significant interaction between the repetition effect in the change detection performance and VSTM capacity ($F = 5.4$, $p < .03$). This difference in the repetition effect was reflected both in the speed and magnitude of the learning. High capacity group showed a significantly improved performance as early as in block 3 ($K = 3.8$ vs $K = 2.8$ for block 3 and new block, respectively, $p = .02$), whereas low capacity group took as long as 8 blocks to show the significant improvement ($K = 2.9$ vs $K = 1.9$ for block 8 and new block, respectively, $p = .04$). Additionally, to assess the magnitude of the learning, we calculated the learning effect as the difference score between the average K score for block 4 through block 10 and the K score for new block.

This difference was positively correlated with individuals' VSTM capacity ($r = .44$, $p < .03$). Taken together, these results suggest that high capacity individuals were faster at learning the contextual cueing and therefore, better at utilizing it to improve their performance to a greater extent.

3. Dissecting the contextual cueing based on VLTM performance

The analyses of the change detection performance during the encoding phase revealed that individuals were able to learn and utilize the contextual cue to improve their performance. However, it is possible that the improved performance was solely driven by the arrays that they could explicitly retrieve the association. To investigate such hypothesis, we classified the repeated arrays based on their performance on the surprise recognition test administered at the end of the experiment. More precisely, the repeated arrays that individuals reported that they had seen were classified as "explicit arrays", and those that individuals reported that they had not seen were classified as "implicit arrays". This separation should allow us to independently assess the improvement in the change detection performance due to the explicit and implicit availability of the representations of the repeated array.

First of all, individuals were better than chance at detecting the repeated arrays, and not surprisingly, high capacity individuals were better at doing so ($p < .001$) (Figure 10D). In separating the "explicit" and "implicit" arrays, high capacity group indicated 10.3 out of 16 repeated arrays as "old" (= explicit) and 5.7 as "new" (= implicit), whereas low capacity group indicated 8.6 out of 16 repeated arrays as "old" and 7.4 as "new" (Figure 10C). This difference was not significant ($p > .05$). Based on this classification of

arrays, the learning effect (i.e. the average K score from block 4 through block 10 - K score for block new) was calculated separately for "explicit" and "implicit" arrays. A repeated-measures ANOVA with 2 factors (VSTM capacity x Retrieval) revealed that the only significant effect was the main effect of VSTM capacity ($F = 6.6$, $p < .03$). This suggests that regardless of the retrieval accessibility, high capacity individuals showed a larger contextual cueing effect. In fact, a simple comparison of the implicit contextual cueing effect revealed that high capacity individuals showed a significantly larger contextual cueing effect ($p < .01$) (Figure 10E). This observation further buttressed by the significant positive correlation between individuals VSTM capacity and implicit contextual cueing effect ($r = .43$, $p < .03$).

Discussion

In this study, we sought to test if the contextual cueing effect, a well-known indirect learning effect, can also be gated by VSTM capacity. Here, we found that, just like direct learning effects, the rate and the amount of the learning effect was determined by individuals' VSTM capacity. Furthermore, this result remained robust even for the arrays that individuals failed to explicitly recognize as "old". These results suggest that even indirect, and arguably, implicit learning is also dictated by the "bandwidth" set by individuals' VSTM capacity.

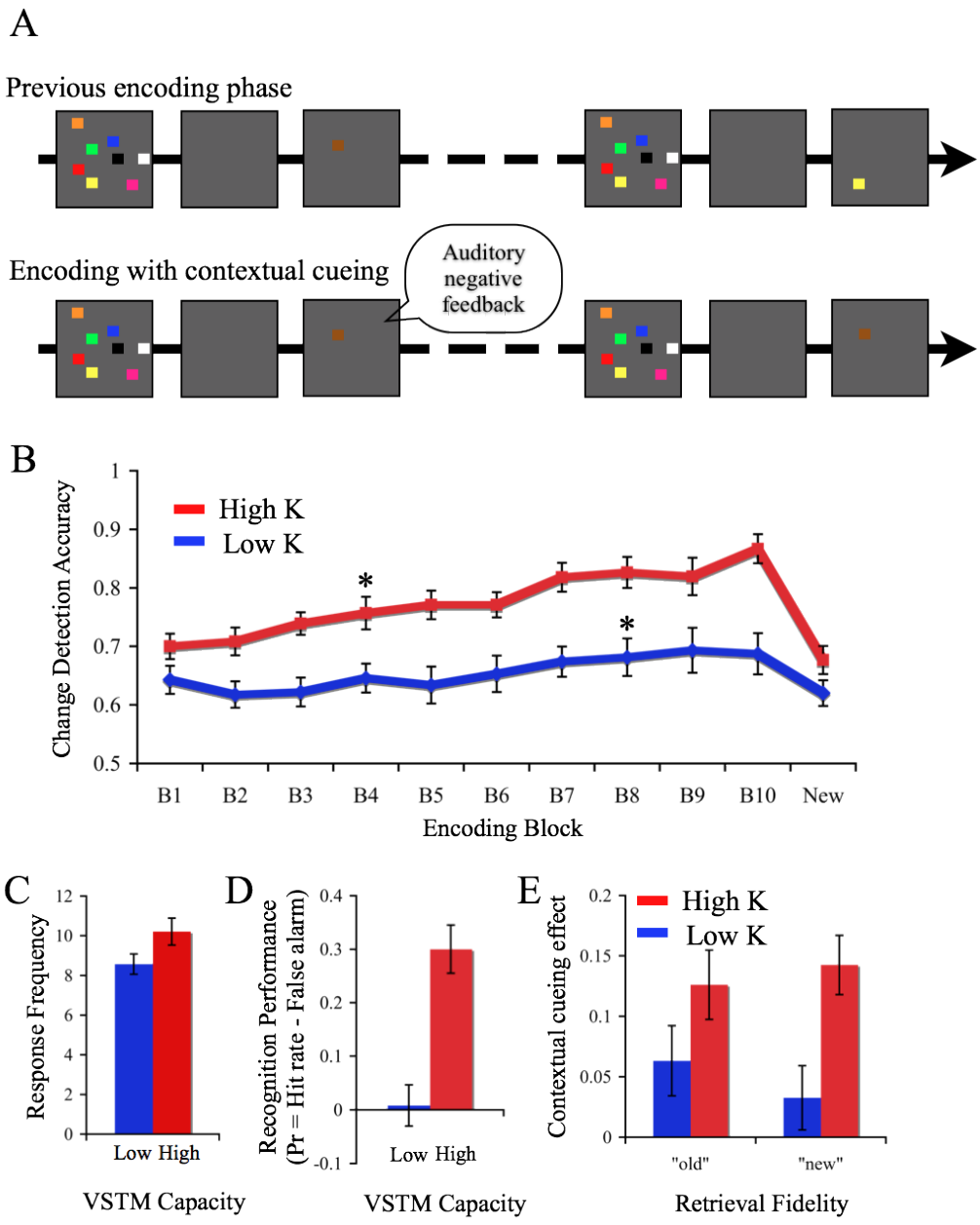

Figure 10. The schematic and the results of Experiment 7
Panel A shows the schematic of the current encoding task in contrast with the previous encoding tasks. Panel B shows the change detection accuracy for high and low capacity (K) groups as a function of the encoding blocks. Panel C shows the response frequency to report "old" for high and low capacity groups during the recognition test. Panel D shows the recognition performance for high and low capacity groups. Panel E shows the contextual cueing effect for high and low capacity groups for the arrays that they reported to have seen (= "old") and not (= "new").

GENERAL DISCUSSION

In this chapter, we sought to expand our theory of direct involvement of VSTM capacity in VLTM encoding by examining the encoding of "implicit" VLTM. Broadly speaking, implicit memory has been defined as the memories that are not explicitly retrieved by the individual, and so far research has focused on demonstrating its qualitative separability from explicit memory. Although there have been recent attempts to find the commonalities between the two memory systems, there hasn't been any research that sought to find the similar principles in their encoding processes. Here, to test if the same "bandwidth" would apply to the encoding of implicit VLTM, we conducted two experiments.

In Experiment 6, we investigated if individuals were capable of detecting the memory traces even if they were not "explicitly" retrievable. The results showed that individuals were able to detect the studied stimuli better than chance even when they indicated that they were "guessing", and thus the memory was not "explicitly retrievable". More importantly, it was the high VSTM capacity individuals that were better at "guessing" the studied stimuli. This suggested that, just like explicit memory, the encoding of implicit memory was also gated by individuals' VSTM capacity.

In Experiment 7, we sought to probe the encoding of implicit memory with an indirect measure, called contextual cueing. By forming the association between the tested item and the studied stimuli, we were able to observe the improvement in change detection performance as stimuli were repeatedly presented. This was in stark contrast to the lack of improvement in change detection performance during encoding in

Experiment 2a and 2b in which such an association was never formed. More critically to our interest, it was again the high VSTM capacity individuals that showed the contextual cueing effect more rapidly and massively. To further validate the "implicitness" of our finding, we extracted the stimuli that were "explicitly" unretrievable by immediately administering a surprise VLTM recognition task. Here, we found that even for the stimuli that were not explicitly recognizable, there was a significant contextual cueing effect, more so for high capacity individuals. Taken together, these results consistently suggest that VSTM capacity serves as the common bottleneck for both explicit and implicit memories.

CHAPTER IV

GENERAL CONCLUSIONS

Our ability to learn from past experiences is fundamental to many aspects of life, and it has been extensively studied in the field of philosophy, psychology and neuroscience. As reviewed in chapter 1, tremendous effort has been made to understand the general mechanisms of learning. In the 1960s, a very intuitive and influential model, called the modal model was proposed, and a significant volume of studies from multiple perspectives has been conducted to test the model since then. The majority of the studies have focused on one of the fundamental assumption that the duration of maintenance (= rehearsal) of information in primary memory determines the successful learning (= encoding into secondary memory) of the information. The evidence so far suggests that the maintenance in primary memory (PM) does play a role in secondary memory (SM) formation, but its effect is not unitary and is far from being the most influential factor on its own (see the levels of processing account, Craik 2002; Lockhart 2002) and in fact, its relatively restricted effect had led some researchers to claim that primary memory maintenance per se is not directly involved in the encoding of SM.

In this thesis, we sought to test another important assumption of the modal model that has not been directly tested. That is, the amount of information represented in PM during encoding determines the amount of information encoded into SM. To directly test this assumption, it is critical to manipulate and keep track of the amount of information represented in PM during encoding. In previous studies, the amount of information that was simultaneously represented in PM was a controlled factor rather than an

experimental factor (e.g. each studied item was sequentially presented with enough temporal isolation to ensure successful maintenance for each item in PM), and thus, the capacity bottleneck at PM was effectively avoided. To directly test its effect, we used visual memory as the model system because the visual analogue of PM capacity limit (i.e. visual short term memory, or VSTM) and the massive SM storage for visual information (i.e. visual long term memory, or VLTM) have been well characterized.

In chapter 2, we first examined the most basic corollary that those who can simultaneously represent more information in VSTM can store more VLTM. To test this, we utilized a well-studied VSTM task called the change detection task as the encoding task in which individuals were introduced to the learning materials. By doing so, we were not only able to directly manipulate the amount of information to be represented in VSTM, but we were also able to keep track of how much information were represented in VSTM for each individual basis. At the end of the encoding phase, individuals' VLTM was tested by a recognition task in which they had to indicate if the stimuli presented were previously studied or not during the encoding phase.

The results of Experiment 1 and 2 revealed that the corollary holds for both object (Experiment 1a and 1b) and relational VLTM (Experiment 2a and 2b) regardless of individuals' intention to learn. More precisely, those who can store more information in VSTM showed better VLTM performance indicating that they encoded more information into VLTM. Critically, this relationship only emerged when individuals' VSTM were saturated by overloading their capacity (i.e. supra-capacity set size such as set size 6 and 8). This finding is very important in rejecting the alternative hypothesis that those with higher VSTM capacity are better at any memory task. The fact that high and low VSTM

capacity individuals performed equally well (but well below ceiling) on VLTM tasks when studied stimuli were presented in sub-capacity set sizes indicated that this relationship is specific to the situation when the amount of information represented in VSTM, and as a consequence the amount of information to be encoded to VLTM, varied across individuals.

In Experiment 3, we sought to directly observe the rate of VLTM encoding. To do so, we asked individuals to study arrays of 8 colored squares that were presented either 10, 20 or 30 times across the encoding phase during which participants simply reported if they have seen the presented array during the experiment. Here, we found that high VSTM capacity individuals showed a steeper improvement of VLTM performance as a function of the number of repetitions. This finding not only helped generalize the tight link between VSTM capacity and VLTM encoding across encoding environments (i.e. change detection task vs simple recognition task), but also provided the direct evidence that VSTM capacity determines the VLTM encoding by imposing the "bandwidth" for the information transfer.

In Experiment 4a and b, we attempted to pinpoint the locus of the interface between VLTM encoding and VSTM processes. Here, unlike the previous experiments, we intended to exploit intra-individual variations in memory performance to obtain a further support for our theory. If the evidence from inter-individual correlations between VSTM and VLTM performance indicate the involvement of a unitary cognitive ability for both performances (in this case, the amount of information simultaneously represented in VSTM) rather than two distinct but correlated memory abilities, we should be able manipulate VLTM performance through VSTM manipulation within individuals.

In Experiment 4a, we parametrically tested the effect of three arguably dissociable stages of VSTM processes, namely, consolidation, maintenance, and test. Interestingly, we found that the VLTM encoding to be specifically linked to the number of encoding opportunities but neither to the duration of maintenance nor the number of tests. More precisely, the improvement in the VLTM performance induced by studying the material multiple times were almost entirely driven by the number of the study opportunities, and neither the increased duration of VSTM maintenance nor the increased number of VSTM tests contributed to the improved performance on the VLTM recognition test. This finding is strongly consistent with the early work on verbal memory and more recent neuroimaging studies that highlighted the disproportionate contribution of the "early" portion of PM maintenance on SM encoding.

Experiment 4b further specified the locus of the interface to be the VSTM consolidation. In this experiment during the encoding phase, we masked the studied stimuli at varied SOAs to manipulate the degree of VSTM consolidation. By doing so, we successfully disrupted the VSTM consolidation, and this disruption was transparent in VLTM performance. More precisely, VSTM performance was the worst when the mask was presented immediately following the offset of the studied stimuli, and it monotonically improved as the presentation of the mask was delayed up to 600ms after the offset. Critically, the SOA function was mirrored in the VLTM performance such that the within-individual correlation of VSTM and VLTM performance was as high as $r = .9$.

In Experiment 5, we attempted to exploit the strong link between VSTM capacity and VLTM encoding to better understand the nature of individual differences in the memory performances. In the VSTM literature, it is well accepted that individual

differences in the amount of information simultaneously represented in VSTM is strongly influenced by individuals ability to regulate their attention to control what information gets into the severely limited capacity of VSTM. In fact, low capacity individuals were found to store "more" task irrelevant information in their VSTM than high capacity individuals. Such evidence leads to an interesting interpretation of individual differences in VSTM capacity that individuals do not necessarily differ in the sheer size of the VSTM capacity, but they differ in how efficient they are at "throttling" the limited resource. If this was the case, our bandwidth hypothesis would predict that it is now the low capacity individuals that encode "more" memories of task-irrelevant information. To test this prediction, we modified the encoding task so that it required individuals to selectively encode the target stimuli amongst task-irrelevant distractors. The result of a surprise VLTM recognition test supported our hypothesis. It was not the low capacity individuals that showed better recognition performance for the task-irrelevant stimuli. This finding added a further credibility to our "bandwidth" hypothesis by demonstrating the direct impact of the attentional ability that underlies the individual differences in VSTM capacity.

In chapter 3, we examined if "implicit" visual long term memory is also encoded with the common "bandwidth" set by VSTM capacity. First, we tested if individuals can correctly identify the studied stimuli even when they report no explicit retrieval (= "guessed"). By modifying our relational memory task based on the previous research, we successfully observed that individuals "guessed" the studied stimuli significantly better than chance. More importantly, it was the high capacity individuals that showed better guessing accuracies. This suggested that, along with explicit VLTM, encoding of implicit

VLTM that is not explicitly accessible is gated by VSTM capacity.

In Experiment 7, we assessed the implicit learning with an indirect measure, the contextual cueing. More precisely, by creating the contextual association for the to-be-tested location and the studied stimuli, we were able to observe the improvement in change detection performance as the function of the repeated exposures. The speed and the amount of the indirect learning effect was again gated by the individuals' VSTM capacity. Further, the link was still existent even when we isolated the learning effect for the stimuli that individuals claimed that they haven't seen.

Taken together, our conclusion is very straightforward. The amount of information successfully consolidated and represented in VSTM during encoding determines the amount of information that can be encoded into VLTM. This link is highly versatile; we observed the relationship regardless of the types of information (object VLTM and relational VLTM), the individuals' intention of learning (incidental learning and intentional learning), and the types of retrieval (explicit retrieval and implicit retrieval). From an information technology standpoint, we can conceive of it as that VSTM determines the "bandwidth" of information transfer into the more durable and high capacity storage of VLTM. Additionally, individuals' variations in the "bandwidth" is better characterized with their ability to "throttle" the bandwidth by attentionally controlling what information gets consolidated through the limited bottleneck.

Implications and future directions

What are the theoretical and applicable implications of the "bandwidth" theory? The theoretical impact of our findings can be found in explaining and extending the

robust relationships between individuals' VSTM capacity and a variety of higher cognitive functions. For instance, fluid intelligence (gF) has been known to be reliably related to the VSTM capacity (Cowan et al. 2005, 2006; Fukuda et al. 2010). For many years, fluid intelligence has been theorized to determine the rate of acquiring crystallized knowledge (i.e. Investment theory by Cattell) although its specific mechanisms have yet to be identified. Here, by demonstrating the direct involvement of VSTM capacity in learning, this study has revealed one potential mechanism through which fluid intelligence has impact on the acquisition rate of crystalized knowledge. Given this context, our findings might provide interesting insight as to how to improve the efficiency of learning. First, we now know that information that overloads VSTM capacity is unlikely to be learned. Furthermore, increasing the number of opportunities to consolidate VSTM representations had a disproportional impact on the successful encoding of VLTM. Such findings regarding the specific limitations and mechanisms of VLTM acquisition can help create a better protocol to improving the efficiency of successful learning.

One fruitful future direction would be to keep expanding the generalizability of the "bandwidth" theory. One of the goals of this dissertation was to test the theory in a variety of contexts so that we can move toward generating a universal theory of learning, and indeed, across all of the experiments, we were able to generalize our findings. However, it is still far from covering all of the types and situations of learning that human are capable of. For instance, our studies are restricted to the learning of visual information. Given the highly consistent limited capacity of the primary memory system across stimulus domains, it is plausible that the same "bandwidth" account holds true in

each stimulus domain. I, however, foresee a major challenge in pursuing this research question. First, it is vital to establish a reliable metric in estimating the amount of information actively represented in PM. Verbal memory literature provides a very salient example. When the capacity of verbal short term memory was initially investigated, digit span task was often used. This task typically reveals that individuals can retain about 7 digits in their PM. However, this estimate changes wildly depending on the exact stimuli and on how the stimuli are presented. More precisely, it is well known that individuals' previous knowledge of the specific stimuli can have a tremendous impact on the sheer amount of information retained in the memory system. Such variability makes it difficult to estimate and control the amount of information represented "actively" in PM during encoding. One potential remedy could be provided by identifying the neural activity that persists through the PM maintenance because its sustained nature of such an activity validates the theoretical assumption that representations in PM are kept active. Clearly, more studies have to be conducted to further expand the universality and exploit the applicability of the "bandwidth" theory of learning.

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